

SPATIAL ECOLOGY AND CONSERVATION OF PARROTS IN NEW CALEDONIA



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Cover artwork: An early depiction of a 'Horned Parrot' by John Latham (1781).

DECLARATION OF ORIGINALITY

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STATEMENT OF ETHICAL CONDUCT

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines set by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

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STATEMENT OF CO-AUTHORSHIP

Several chapters of this thesis are composed of manuscripts that have either been published, submitted to journals, or are in preparation to be submitted. I am the first author of the manuscripts that comprise the core of this thesis, and I co-authored the manuscript that is included in the Appendix. I took part in the collection of field data for each manuscript and was responsible for the writing and analyses associated with each of the central chapters. I played a role in developing and operating the wildlife surveillance system that is described in the Appendix. I also supplied the illustration of the system and contributed to the text.

A number of individuals were granted co-authorship in acknowledgement of their contributions to the core chapters. Jörn Theuerkauf supervised the research and provided advice on GIS and statistical analysis. Jörn Theuerkauf, Sophie Rouys, and Roman Gula contributed observational data from various sites on the mainland, including Parc Provincial de la Rivière Bleue. Vivien Chartendrault, Nicolas Barré, and Frédéric Desmoulins provided data from point counts conducted in the Northern and Southern Province. Maurice Saoumoé, Ludovic Verfaille, and Nicolas Barré supplied data from distance sampling surveys on Ouvéa. Emilie Baby and Laetitia Moutin contributed data from distance sampling surveys at Parc Provincial de la Rivière Bleue. All co-authors were given the opportunity to comment on manuscript drafts.

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Andrew Legault

March 2012

CONDITIONS OF RESEARCH

This research was carried out under a formal agreement between the University of Tasmania and the Museum and Institute of Zoology (Polish Academy of Sciences), and was co-supervised by Assoc. Prof. Alastair Richardson (UTAS), Assoc. Prof. Jörn Theuerkauf (PAS), and Prof. Susan Jones (UTAS).

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New Caledonia's parrots face a variety of threats, and the populations of several species appear to be in decline. However, it is difficult to determine the cause or extent of their declines due to a scarcity of ecological data. Accordingly, this research aims to contribute to the conservation of parrots in New Caledonia by studying their spatial ecology. This thesis documents the habitat preferences of parrots on the main island of New Caledonia in relation to environmental variables on a large and small scale. Information about their activity patterns and flock sizes is provided, and an optimised method of surveying parrots is described. In addition, ecological niche models are used to infer the distribution and population size of parakeets.

New Caledonian Rainbow Lorikeets (*Trichoglossus haematodus deplanchii*) were frequently encountered in this study, and were successful in a variety of habitats, including urban areas. New Caledonian Parakeets (*Cyanoramphus saisseti*) and Horned Parakeets (*Eunymphicus cornutus*) were less common, and appeared to be more specialised in their habitat requirements. Relatively large and intact patches of rainforest on oligotrophic soils at intermediate altitudes provided important habitat for both of these species, and would be appropriate areas for conservation given their vulnerability to mining activities.

New Caledonian Parakeets foraged mainly at low canopy heights, and were regularly observed at the edge of forest, in slope forest, or in maquis (shrubland). In comparison, Horned Parakeets tended to forage at greater heights, favoured valley forest over slope forest, and avoided open habitats. The observed patterns of vertical stratification and habitat segregation probably help to prevent interspecific competition.

Flocks of parakeets usually consisted of one or two birds, and their size remained relatively consistent during the day, and throughout the year. Most Rainbow Lorikeet flocks contained only a few individuals, though some had up to 40 birds. All species had bimodal activity patterns.

Distance sampling was found to be suitable for surveying parakeets in New Caledonia, but surveys should be standardised to facilitate comparison between different areas and time periods.

Parakeets in New Caledonia appear to have small populations, and their distributions are expected to contract as a result of climate change. Ouvéa Parakeets (*Eunymphicus uvaensis*) may be particularly vulnerable in this regard. This study indicates that the current reserve network provides insufficient protection for parakeets. There is a need to increase the area devoted to reserves, provide corridors for dispersal, manage introduced species, and raise environmental awareness in the region.

CHAPTER 1 INTRODUCTION

This chapter provides background information about New Caledonia, beginning with its location, climate, and geological history. Attention is drawn to the originality and diversity of the New Caledonian flora and fauna, and the origins of the New Caledonian biota are explored. An overview of the different habitat types in New Caledonia is provided, along with a description of the New Caledonian parrots and their presumed origins. A summary of the threats facing the New Caledonian avifauna is also included, and the specific objectives of this study are outlined.

CHAPTER 2 LARGE-SCALE HABITAT SELECTION BY PARROTS IN NEW CALEDONIA

This chapter examines the selection of habitat by parrots on the main island of New Caledonia in relation to vegetation, forest cover, forest size, altitude, rainfall, and soil. The critical habitats for New Caledonian parrots are evaluated across a broad spatial extent, and their importance for conservation is discussed.

CHAPTER 3 TEMPORAL VARIATION IN FLOCK SIZE AND HABITAT USE OF PARROTS IN NEW CALEDONIA

In this chapter, the selection of habitat by parrots is examined at a small scale, particularly with respect to different vegetation types. Seasonal habitat selection is analysed as well as selection relative to forest edges. The activity patterns, flock sizes (including daily and monthly variations), and foraging heights of each species are also considered. The implications of these findings are discussed with particular emphasis upon each species' relative susceptibility to habitat modification.

CHAPTER 4 STANDARDISING DISTANCE SAMPLING SURVEYS OF PARROTS IN NEW CALEDONIA

The primary aim of this chapter is to provide details of a standardised method for surveying parrots in New Caledonian rainforests. Distance sampling is used to estimate parrot densities at several IBAs (Important Bird Areas) in New Caledonia. These estimates provide a foundation for future surveys, and can be used as a comparative reference for parakeets inhabiting other regions. The advantages of carrying out standardised surveys are discussed in light of the need to accurately estimate parrot populations in New Caledonia.

CHAPTER 5 USING ECOLOGICAL NICHE MODELS TO INFER THE DISTRIBUTION AND POPULATION SIZE OF PARAKEETS IN NEW CALEDONIA

In this chapter, ecological niche models are used to infer the current and future distribution of parakeets in New Caledonia. In addition, the population size of each species is assessed by evaluating the relationship between local abundance and modelled habitat suitability. The long-term suitability of the existing reserve system is critically analysed and discussed.

CHAPTER 6 IMPLICATIONS FOR CONSERVATION

The main findings of this study are brought together in this chapter, and conservation measures are proposed which should help to ensure the survival of New Caledonia's parrots.

APPENDIX AN AUDIO/VIDEO SURVEILLANCE SYSTEM FOR WILDLIFE

This supplementary manuscript describes an audio/video recording system used to record and monitor nesting parakeets, and other endemic birds, in the rainforests of New Caledonia. The utility of this system is discussed, particularly with respect to assessing nest predation, and studying the behaviour of nesting birds and other animals in the wild.

Note: Most chapters have been prepared for publication, therefore some overlap in the content of each chapter is to be expected.

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CHAPTER 1

INTRODUCTION

LOCATION AND CLIMATE

New Caledonia is an isolated archipelago located in the southwest Pacific Ocean, about 1,200 km east of Queensland, Australia. The main island, 'Grande Terre', is approximately 400 km long by 50 km wide, and is oriented in a northwest/southeast direction (Figure 1.1). A number of small islands extend along its axis to the north (Île Balabio, Île Baaba, and Îles Bélep) and south (Île Ouen, Île des Pins). This entire collection of islands is surrounded by an extensive barrier reef, which encloses a vast lagoon. The Loyalty Islands lie parallel to the main island, about 100 km to the northeast. From north to south, the main landforms in the Loyalty Islands group are Ouvéa, Lifou, Tiga, and Maré. The rest of the New Caledonian archipelago is comprised of numerous small, isolated islets and reefs.

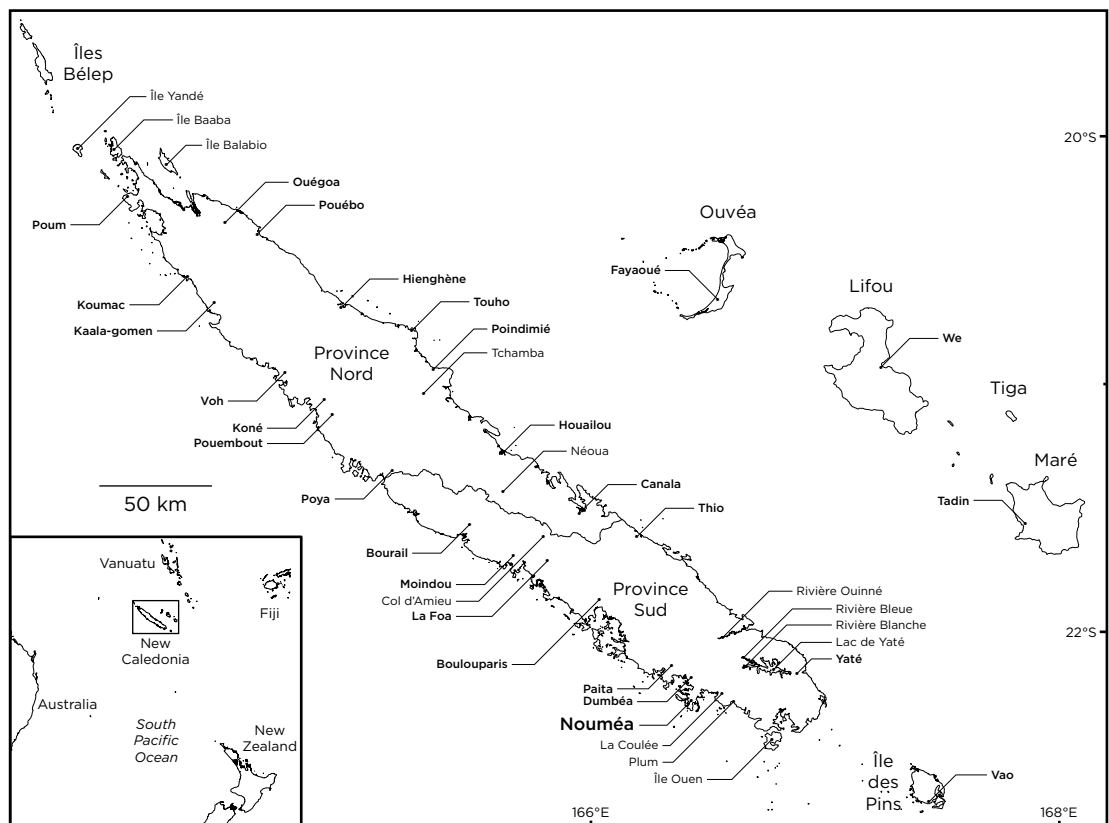


Figure 1.1: Map of New Caledonia showing the main islands, towns (*bold*), and various localities mentioned in the text. Refer to Figure 5.1 for the location of reserves and Important Bird Areas (IBAs).

A central chain of mountains runs lengthwise along the main island (Figure 1.2), with several peaks exceeding 1,500 m, the highest of which is Mont Panié (1,628 m). There is a marked asymmetry between the topography of the eastern and western sides of the island. In the east, the mountains drop abruptly towards the sea, and are dissected by deep, narrow valleys formed by numerous short rivers and streams. In the west, the mountains taper gradually into rolling hills and eventually transition into broad coastal plains. Owing to the island's relief, and the prevailing southeast trade winds, precipitation is unevenly distributed on the island (Figure 1.3). In the far south, and along the windward eastern slopes, annual precipitation occasionally reaches in excess of 4,000 mm, while the leeward coastal plains in the west generally receive less than 1,500 mm of precipitation per year (ORSTOM 1981). Rainfall in the low-lying Loyalty Islands is comparable to that of the drier western parts of the mainland.

The annual rainfall pattern in New Caledonia is highly irregular, making it difficult to identify a clear separation between seasons. The heaviest rains occur during the warmest time of the year, roughly from December to April, and are typically associated with the movement of nearby pressure systems or cyclones. The length of the dry season varies, but the months of September to November tend to receive the least rainfall. Rainfall is moderate during the remainder of the year, when temperatures tend to be cooler. Mean annual temperatures range between 22 and 24°C, yet temperatures can vary significantly between sites (ORSTOM 1981). The east coast is generally cooler than the west as it is exposed to the prevailing winds. There is also a strong temperature gradient between low and high altitude sites, with frost occurring on some peaks at certain times of the year (David *et al.* 1995).

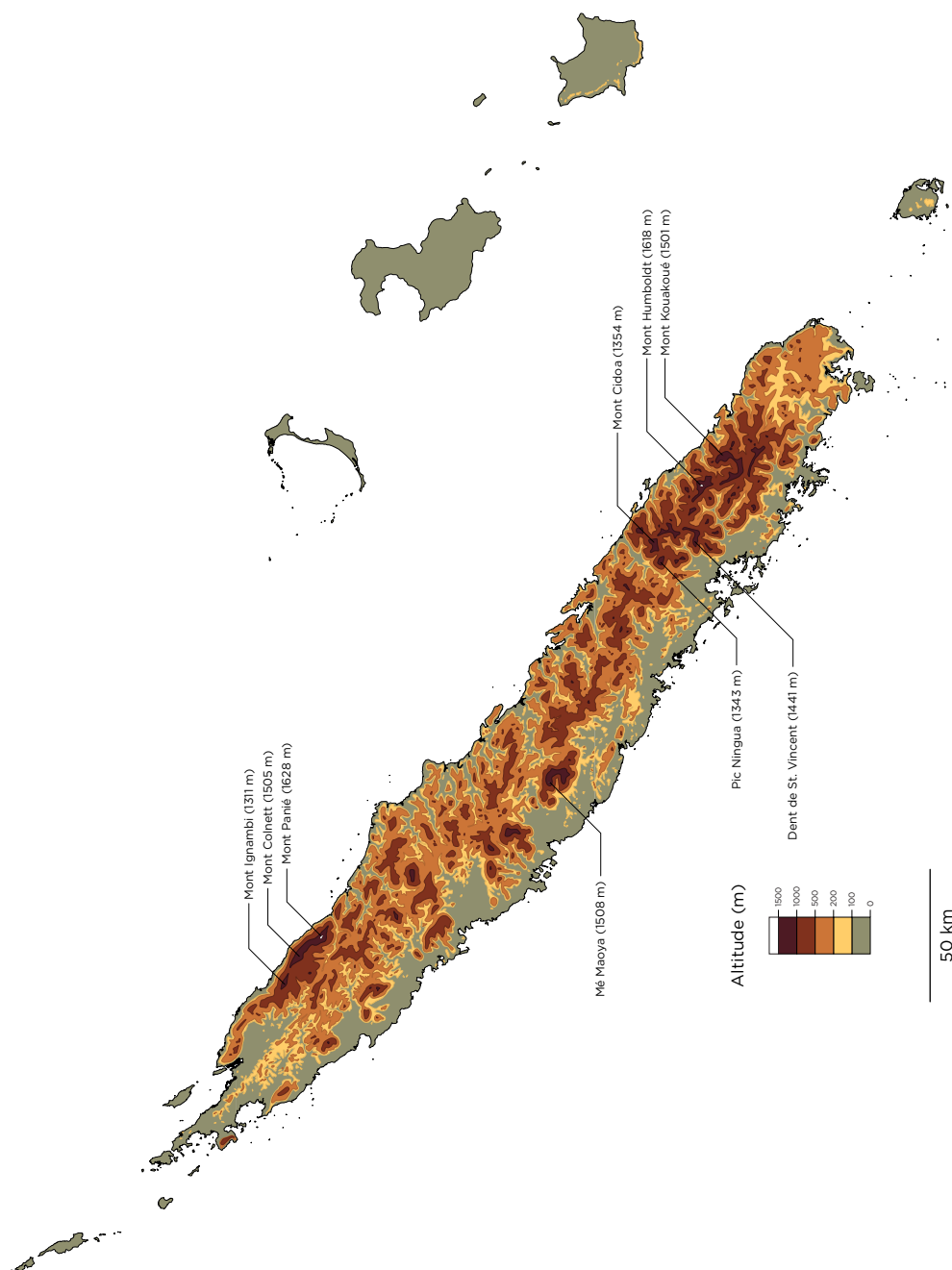


Figure 1.2: Map of the topography of New Caledonia, with most of the highest peaks labelled. Adapted from ORSTOM (1981).

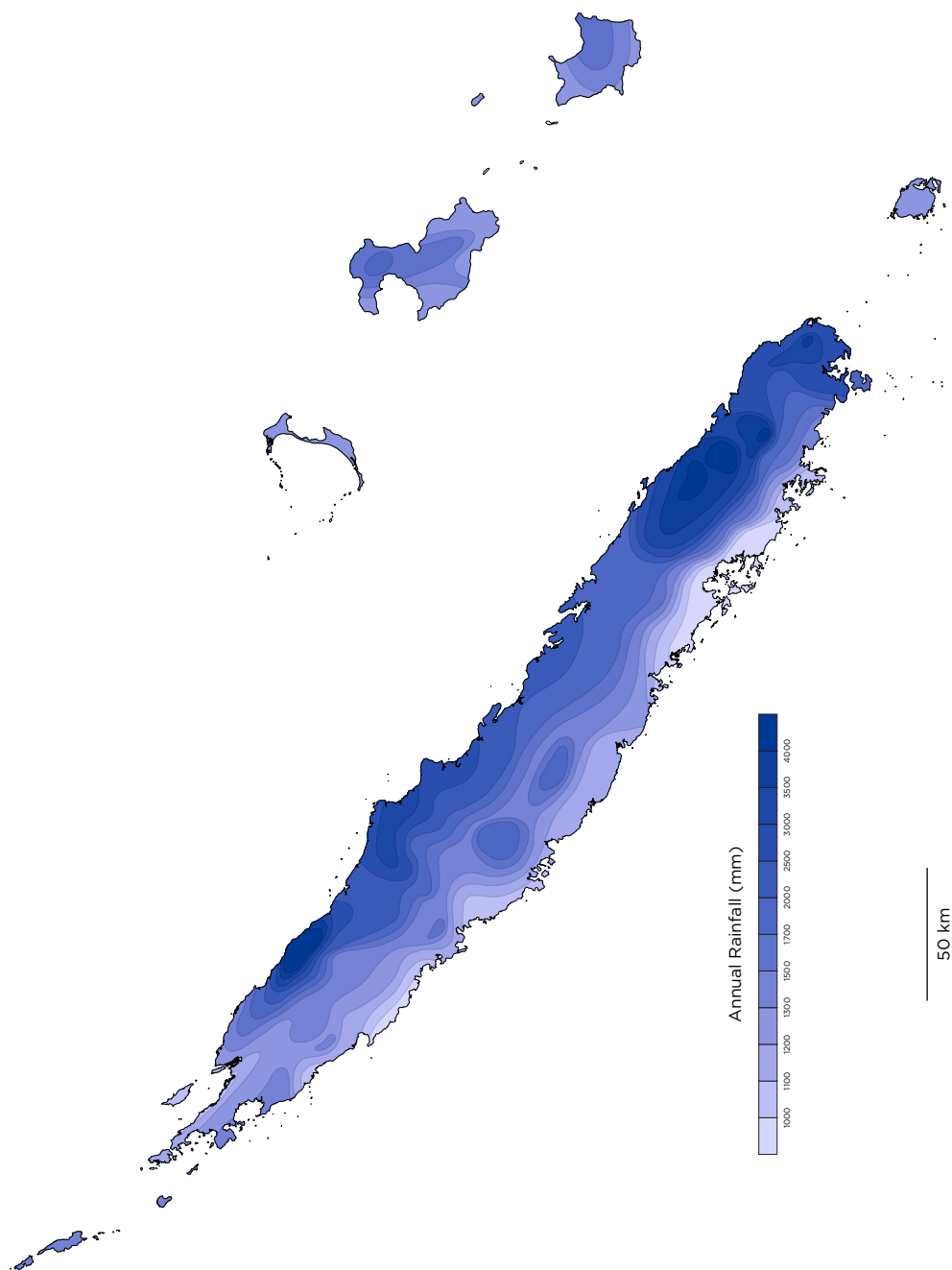


Figure 1.3: Map showing the mean annual rainfall in New Caledonia, based on averages from 1956-1975, Adapted from ORSTOM (1981).

The New Caledonian mainland, and adjacent islands to the northwest (Île Balabio, Île Baaba, and Îles Bélep) and southeast (Île Ouen, Île des Pins), represent some of the oldest landforms in the southwest Pacific. The islands lie atop the Norfolk Ridge, which runs southward to form part of a large continental plateau bearing New Zealand (Cluzel *et al.* 2001). This vast expanse of thinned continental crust, commonly referred to as Zealandia (Figure 1.4), once formed a terrestrial link between New Caledonia, New Zealand, and Australia (Luyendyk 1995, Mortimer 2004, Trewick *et al.* 2007). Its connection with Australia was severed between 84 to 61 Ma ago, during the breakup of Gondwana (Ladiges & Cantrill 2007). As Zealandia rifted away from the east coast of Australia, it split into several fragments, and began to subside as it stretched and thinned out (Ladiges & Cantrill 2007, Trewick *et al.* 2007). As a consequence, most of Zealandia now lies 2,000 to 3,000 m below sea level (Trewick *et al.* 2007).

The region of Zealandia that eventually became New Caledonia appears to have been at least partially submerged at some point during the Paleogene, as indicated by the presence of marine limestones and cherts (Brothers & Lillie 1988, Pelletier 2007, Heads 2008). In the Eocene, collision of the basement terranes with an island arc to the northeast (probably the Loyalty Ridge) led to the emplacement of a large ultramafic ophiolitic nappe (*i.e.* an obducted¹ slice of oceanic crust) over much of the mainland (Chevillotte *et al.* 2006, Grandcolas *et al.* 2008, Heads 2008, Neall & Trewick 2008). This thick sheet of ultramafic rocks has been substantially eroded since its establishment, but still covers the southern third of the mainland, reaching Île des Pins in the south, and extends as a series of klippe² along the western half of the mainland, as far north as Îles Bélep (Cluzel *et al.* 2001, Pelletier 2007). Soils derived from these ultramafic substrates (*e.g.* acric ferralsols; Figure 1.5) often have high levels of nickel, manganese, and magnesium, and are typically deficient in phosphorus, potassium, nitrogen, and calcium (Jaffré 1980, 1995, McCoy *et al.* 1999).

¹ Obduction occurs when oceanic crust is thrust over continental crust, whereas subduction occurs when oceanic crust slides beneath continental crust, or other oceanic crust.

² Klippes are remnants of the initial nappe that have become isolated due to erosion.

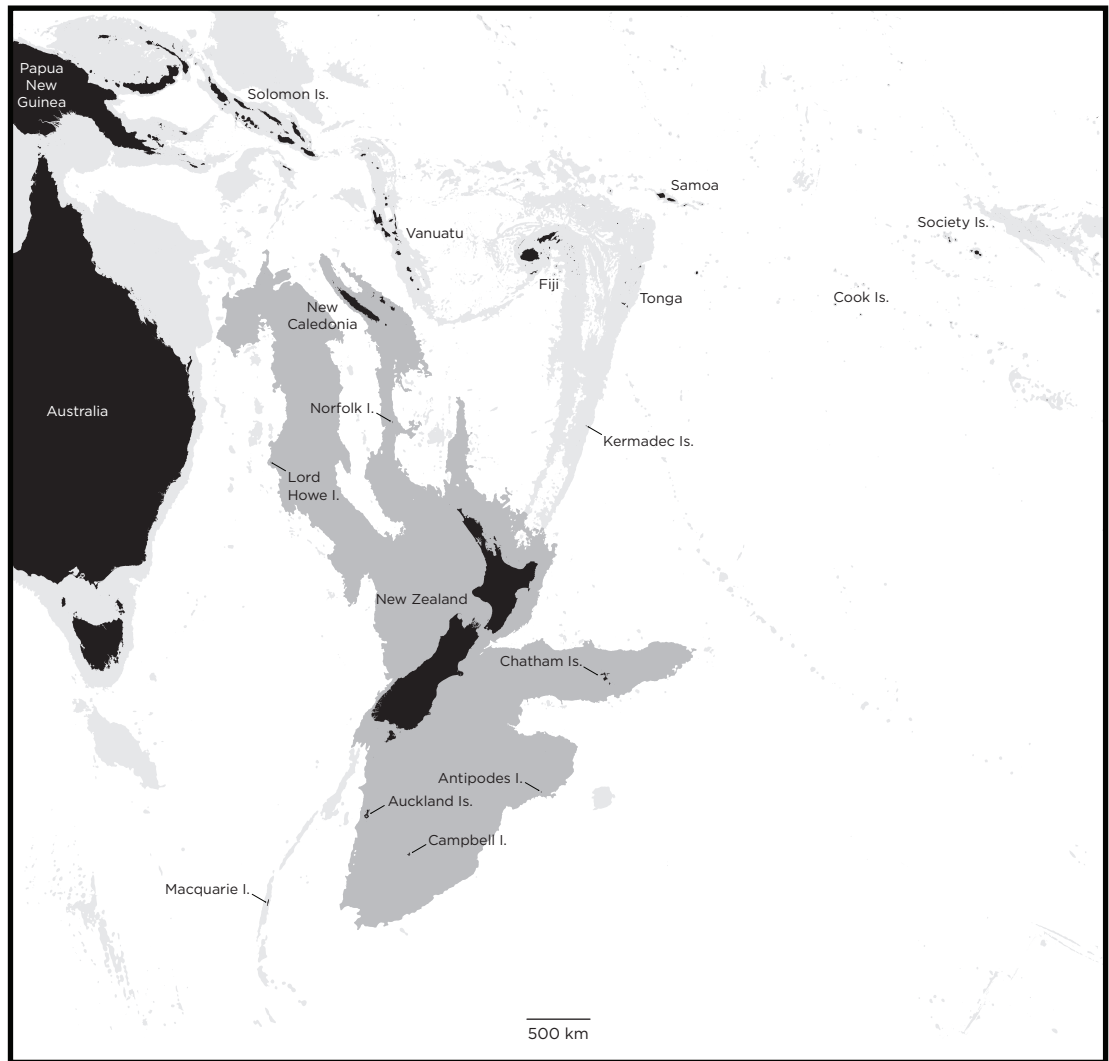


Figure 1.4: The southwest Pacific showing the location of New Caledonia and other major land masses mentioned in the text (black). A 2,500 m isobath is used to depict the extent of Zealandia (dark grey) and other continental/arc crust in the region (light grey). Bathymetric data are based on the GEBCO_08 Grid v. 20091120 (www.gebco.net).

Running parallel to, and east of, the Norfolk Ridge is the Loyalty Ridge (Figure 1.6), a largely submarine feature that appears to be the remains of an ancient island arc (Cluzel *et al.* 2001, Crawford *et al.* 2003, Pelletier 2007, Heads 2008). The initial separation of these two ridges probably began in the Late Cretaceous, resulting in the formation of the South Loyalty Basin (Heads 2008). During the Eocene, the Loyalty Ridge may have been attached to the Vitiaz Arc (Solomon Islands, Vanuatu, Fiji) in the east (Crawford *et al.* 2003, Heads 2008). About 35 Ma ago, the subduction of the South Loyalty Basin may have temporarily brought the Loyalty Ridge and Norfolk Ridge together again, after 30 million years of isolation (Heads 2008, Neall & Trewick 2008).

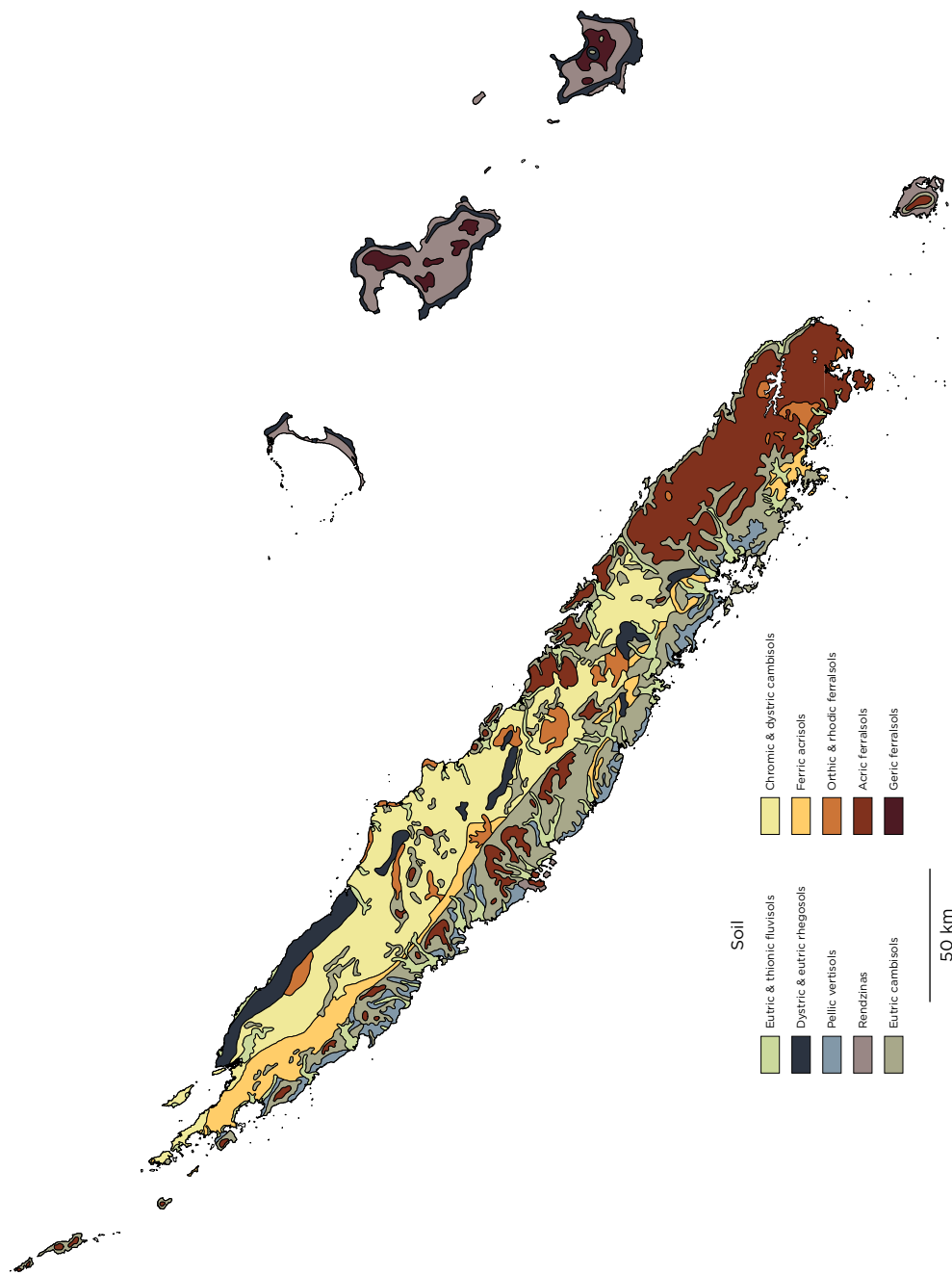


Figure 1.5: Map showing the distribution of different soil types in New Caledonia. Adapted from ORSTOM (1981).

The Loyalty Ridge is characterised by a chain of seamounts that emerge in several locations to form the Loyalty Islands, a group of uplifted coral atolls that formed in the Late Miocene to Pleistocene upon a base of volcanic rock (Guyomard *et al.* 1996, Crawford *et al.* 2003, Pelletier 2007, Heads 2008). The emergence of the Loyalty Islands appears to have begun during the Pleistocene, due to lithospheric flexure, and their upheaval continues to the present (Dubois *et al.* 1973, Pelletier 2007). The soils of the Loyalty Islands are mainly calcareous, although shallow ferralitic/allitic soils (rich in aluminium and iron oxides) can be found in the interior of Lifou and Maré (Figure 1.5).

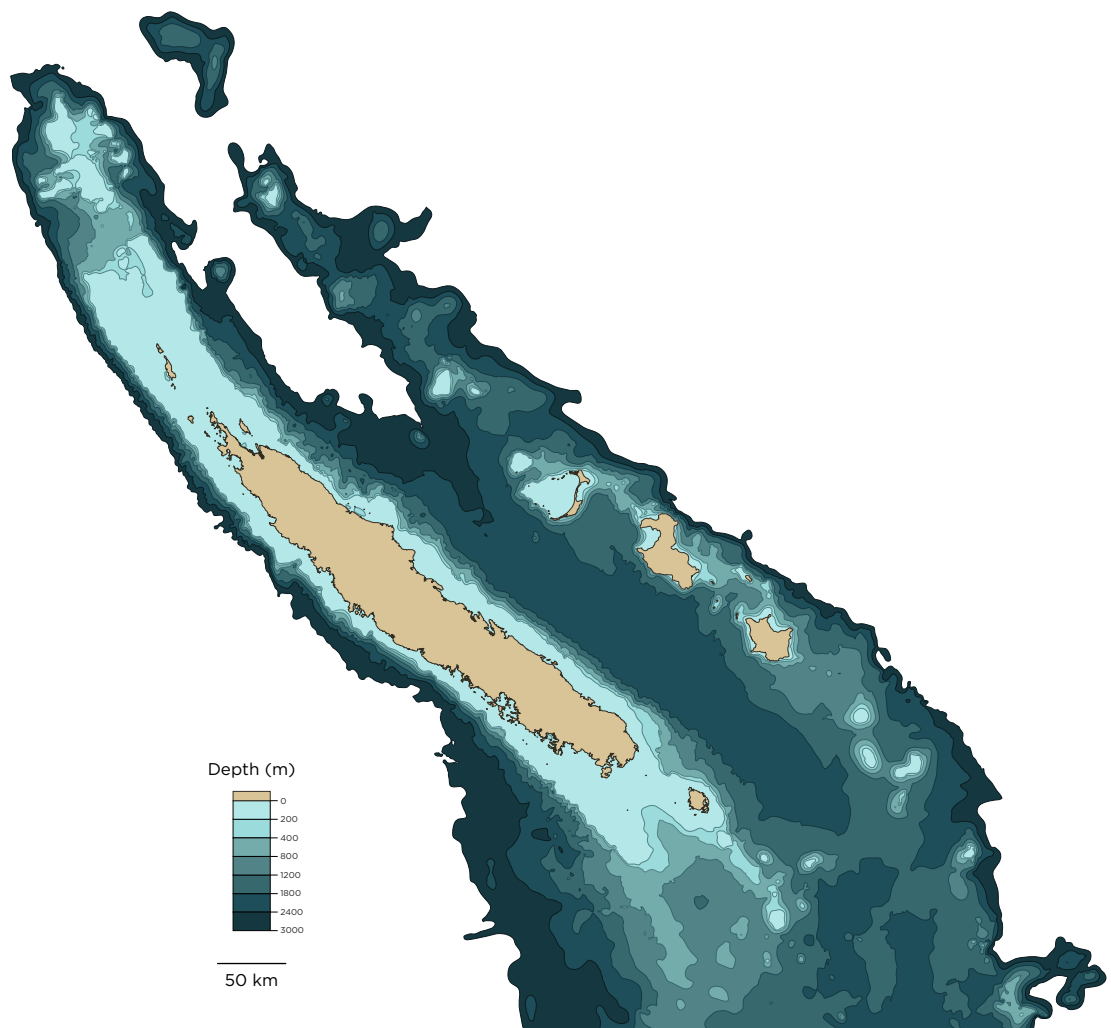


Figure 1.6: Bathymetric map of New Caledonia showing depths to 3,000 m. The 200 m isobath approximately marks the extent of the lagoon surrounding the mainland. Note also the presence of the Loyalty Basin separating the Norfolk and Loyalty Ridges. Bathymetric data are based on the GEBCO_08 Grid v. 20091120 (www.gebco.net).

FLORAL DIVERSITY AND HABITATS

New Caledonia is renowned for its exceptional biodiversity and high potential for conservation (Myers *et al.* 2000). Considering the relatively small size of the archipelago (ca. 19,000 km²), the flora is extremely rich and original, with an estimated 3,261 species of native vascular plants, over 74% of which are endemic (Jaffré *et al.* 2001b). The distinctive nature of the flora is also apparent at higher taxonomic levels, with 106 of the 806 genera, and 5 of the 194 families of vascular plants being endemic to the region (Morat 1993a, Jaffré *et al.* 2001b). The only other countries with endemic plant families are Australia, Madagascar, and Fiji (Mittermeier *et al.* 1996). In fact, the composition of the flora is so extraordinary that various authors have recognised New Caledonia as a phytogeographic region in itself (Morat 1993a).

New Caledonia's native terrestrial vegetation (Figure 1.7) can be separated into four distinct habitat types (Jaffré 1993): rainforest (Figures 1.8-1.12), maquis (Figures 1.8 & 1.13), dry sclerophyll forest (Figure 1.13), and savannah (Figure 1.14). Mangroves (Figure 1.15) also occur in some coastal locations, particularly along the west coast, and plantations of introduced pine and coconut are common (Figure 1.15).

Rainforest is a dense, evergreen formation composed of a wide variety of medium to large trees (*Agathis*, *Araucaria*, *Calophyllum*, *Montrouzieria*, *Pancheria*, *etc.*), giant tree ferns (*Angiopteris*, *Cyathea*, *Dicksonia*, *etc.*), and tall palms (*Basselinia*, *Burretio kentia*, *Kentiopsis*, *etc.*) that form a canopy about 20 to 25 m in height, with some emergents (e.g. *Araucaria* and *Agathis*) towering well above the rest of the forest (Jaffré & Veillon 1989, Jaffré 1995, Jaffré & Veillon 1995). The understorey includes a mixture of ferns, palms, epiphytes, lianas, and numerous small trees and shrubs (*Austromyrtus*, *Cupaniopsis*, *Melicope*, *Pandanus*, *Psychotria*, *etc.*) (Jaffré & Veillon 1995). This diverse habitat comprises 2,012 species of vascular plants (82.2% endemic) from 483 genera and 138 families, and includes all five of New Caledonia's endemic plant families (Amborellaceae, Oncothecaceae, Paracryphiaceae, Phellinaceae, and Strasburgeriaceae) (Jaffré *et al.* 2001b).

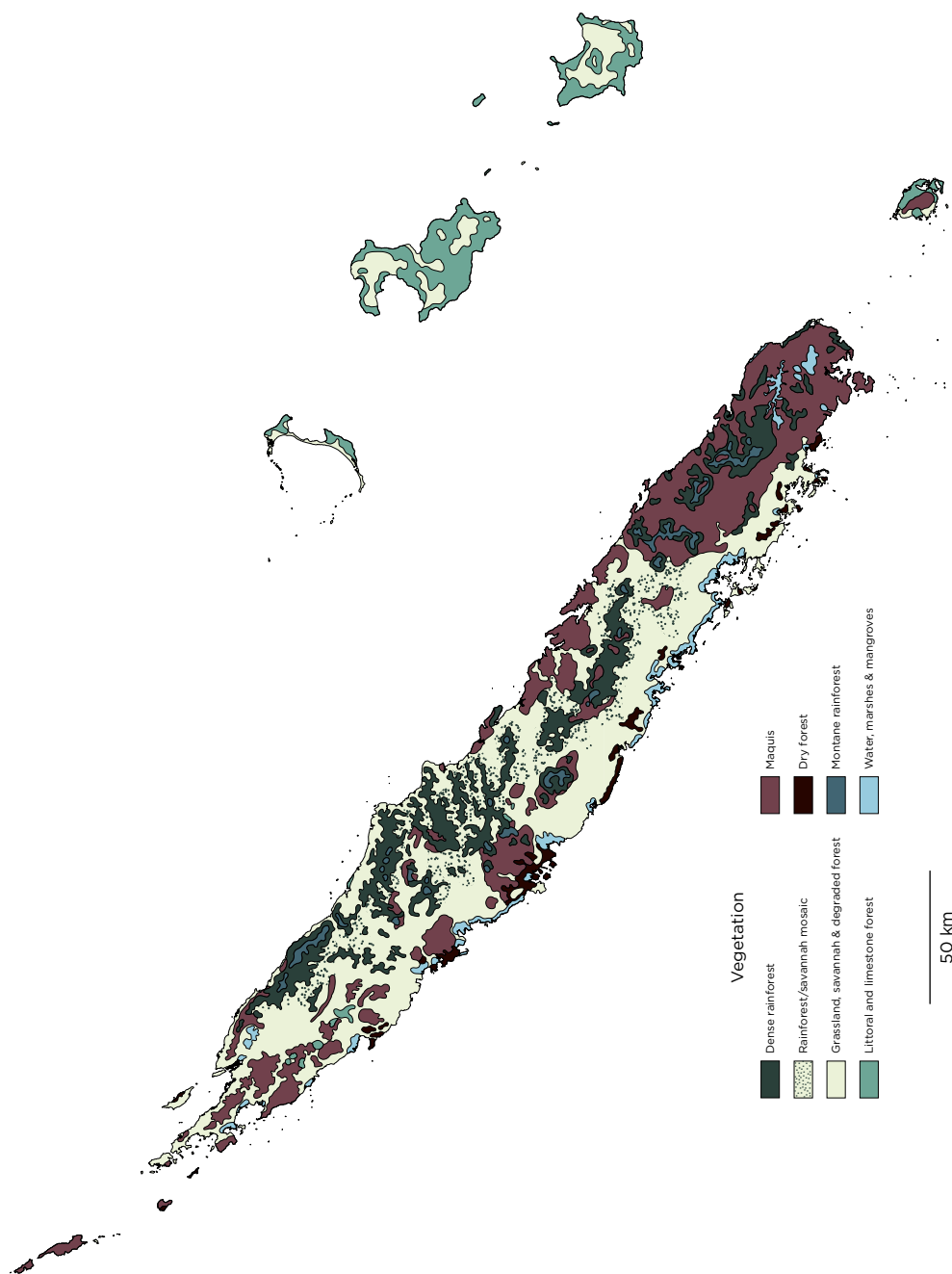


Figure 1.7: Map showing the major vegetation types that occur in New Caledonia. Adapted from ORSTOM (1981).

Rainforest covers about 3,350 km² (20%) of the mainland (Jaffré 1993), and is mainly located in the valleys and steep slopes of the central mountain chain, particularly along the eastern half of the island. Suitable conditions for rainforest begin around 100-300 m above sea level, where annual rainfall is typically over 1,500 mm (Jaffré 1995). Rainforest takes on a distinct appearance above 900-1,000 m, and occasionally, above 600 m along the wetter, eastern slopes (Mueller-Dombois & Fosberg 1998, Nasi *et al.* 2002). These montane rainforests (Figure 1.12) have a low, discontinuous canopy comprised of relatively short trees (3-8 m) with spindly trunks, and a relatively dense understorey (Jaffré 1995).

Rainforest is found on a variety of different substrates, covering approximately 1,800 km² on acidic rocks, 1,200 km² on ultramafic rocks, and 900 km² on calcareous rocks (including about 550 km² on the Loyalty Islands) (Jaffré 1993, Jaffré *et al.* 1997). Rainforests on ultramafic substrates (1,360 species from 400 genera and 118 families) and acidic substrates (1,367 species from 431 genera and 127 families) are much more diverse than rainforests on calcareous substrates (225 species from 155 genera and 74 families). The ultramafic rainforest flora has a higher rate of specific endemism (82.4%) than rainforests on acidic substrates (76.7%) or calcareous substrates (48.0%), and is also more original at higher taxonomic levels (Jaffré *et al.* 1997).

Maquis is a low, dense, sclerophyllous vegetation formation comprised mainly of light-demanding woody shrubs and sedges that may be locally dominated by an arborescent layer of *Araucaria* spp. or *Agathis ovata* (Chazeau *et al.* 1994, Jaffré 1995). With 1,144 species of vascular plants from 321 genera and 103 families, the maquis flora is not as rich as rainforest, but it is more original, with a specific endemism of 88.8% (Jaffré *et al.* 2001b). Maquis covers about 4,500 km² (27%) of the mainland, and develops over a wide range of altitudes and under various climatic and edaphic conditions, but it is typically associated with ultramafic substrates (Figure 1.8) (Jaffré 1992, Morat 1993a, Read *et al.* 2006). For the most part, maquis is a secondary formation resulting from the removal of the original forest cover by recurrent fires (Jaffré *et al.* 2010). Ultramafic vegetation appears to undergo a post-fire succession from low, open maquis to tall, closed maquis, before developing into forest, and eventually rainforest (Jaffré 1980, McCoy *et al.* 1999). This succession from maquis to structurally complex rainforest has been estimated to take over 250 years (McCoy *et al.* 1999).

In its natural state, dry sclerophyll forest is a closed formation dominated by semi-deciduous trees, with a canopy reaching 10 to 15 m in height (Morat 1993a, Bouchet

et al. 1995, Veillon *et al.* 1999). Vines and woody sclerophyllous shrubs form the understorey, along with a herbaceous layer of sedges and grasses (Morat 1993a, Bouchet *et al.* 1995, Veillon *et al.* 1999). The forest is almost exclusively associated with non-ultramafic, sedimentary substrates (e.g. chert, sandstone, limestone) (Veillon *et al.* 1999). Sclerophyll forest comprises 438 species of vascular plants belonging to 253 genera and 93 families (Jaffré *et al.* 2001b). Some of the more common plant families in this habitat type are the Ebenaceae, Euphorbiaceae, Myrtaceae, and Sapindaceae (Bouchet *et al.* 1995). These forests are not nearly as diverse as rainforest or maquis, but they harbour 252 endemic species of vascular plants (Jaffré *et al.* 2001b), including 60 flowering plants that are not found anywhere else (Gillespie & Jaffré 2003), such as the monotypic genus *Captaincookia* (Bouchet *et al.* 1995). To some extent, the relatively low diversity of sclerophyll forest can be attributed to extensive habitat destruction (Lowry 1998). Initially occupying all of the dry, low-lying areas of the west coast (*i.e.* about 4,500 km² under 300 m a.s.l.), sclerophyll forest has been drastically reduced to about 2% of its former extent (Chazeau *et al.* 1994, Bouchet *et al.* 1995, Veillon *et al.* 1999). Less than 100 km² of intact sclerophyll forest now remains, and open and secondary forests account for another 250 km² (Bouchet *et al.* 1995, Veillon *et al.* 1999).

Savannah is an open grassland formation, often wooded with 'niaouli' (*Melaleuca quinquenervia*), a small to medium-sized native paperbark tree up to 20 m in height (Jaffré *et al.* 1994). This secondary vegetation type arises from the destruction of either sclerophyll forest or rainforest on non-ultramafic substrates (Jaffré *et al.* 1994). The spread of savannah appears to have begun about 3,000 years ago, with the arrival of the initial Lapita settlers, who used fire to clear and maintain an open landscape (Stevenson 2004). Its distribution was greatly extended by European colonisers, who cleared vast tracts of native vegetation, primarily dry sclerophyll forest, to allow for agriculture and cattle ranching (Bouchet *et al.* 1995, Stevenson 2004). Savannah is now widespread in New Caledonia, covering an approximate area of 6,000 km² (36% of the mainland), from the coastline to about 700 m above sea level (Jaffré *et al.* 1994). Despite its broad distribution, savannah is comprised of merely 81 native vascular plant species, belonging to 62 genera and 20 families (Jaffré *et al.* 2001b). Only seven endemic species occur in savannah (Jaffré *et al.* 2001b), and these probably originate from other vegetation types growing nearby (Jaffré *et al.* 1994).



Figure 1.8: Images of Parc Provincial de la Rivière Bleue: ultramafic terrain above the Rivière Bleue (top left) and Forêt Noyée (top right); rainforest along the banks of the Rivière Bleue (bottom right); and maquis by a small waterfall (bottom left).



Figure 1.9: Images of Parc Provincial de la Rivière Bleue (continued): 'Le Grand Kaori' (*Agathis lanceolata*), New Caledonia's largest tree (top left); tree hollow (top right); and rainforest vegetation along the Rivière Bleue (bottom).



Figure 1.10: Images of Parc Provincial de la Rivière Bleue (continued): rainforest with emergent *Araucaria* trees (top); rainforest understorey (bottom right); streamside vegetation (bottom left).



Figure 1.11: Rainforest vegetation at Parc des Grandes Fougères (top left). The canopy is comprised of a variety of palms (top right*), large trees (bottom right), and giant tree ferns (bottom left). Credit: Mélusine Lefebvre*



Figure 1.12: Montane rainforest on Mont Panié at 1600 m (top*) and Mont Mou (bottom right*), and mixed rainforest along the banks of the Rivière Tao, adjacent to Mont Panié (bottom left). Credit: Jörn Theuerkauf*

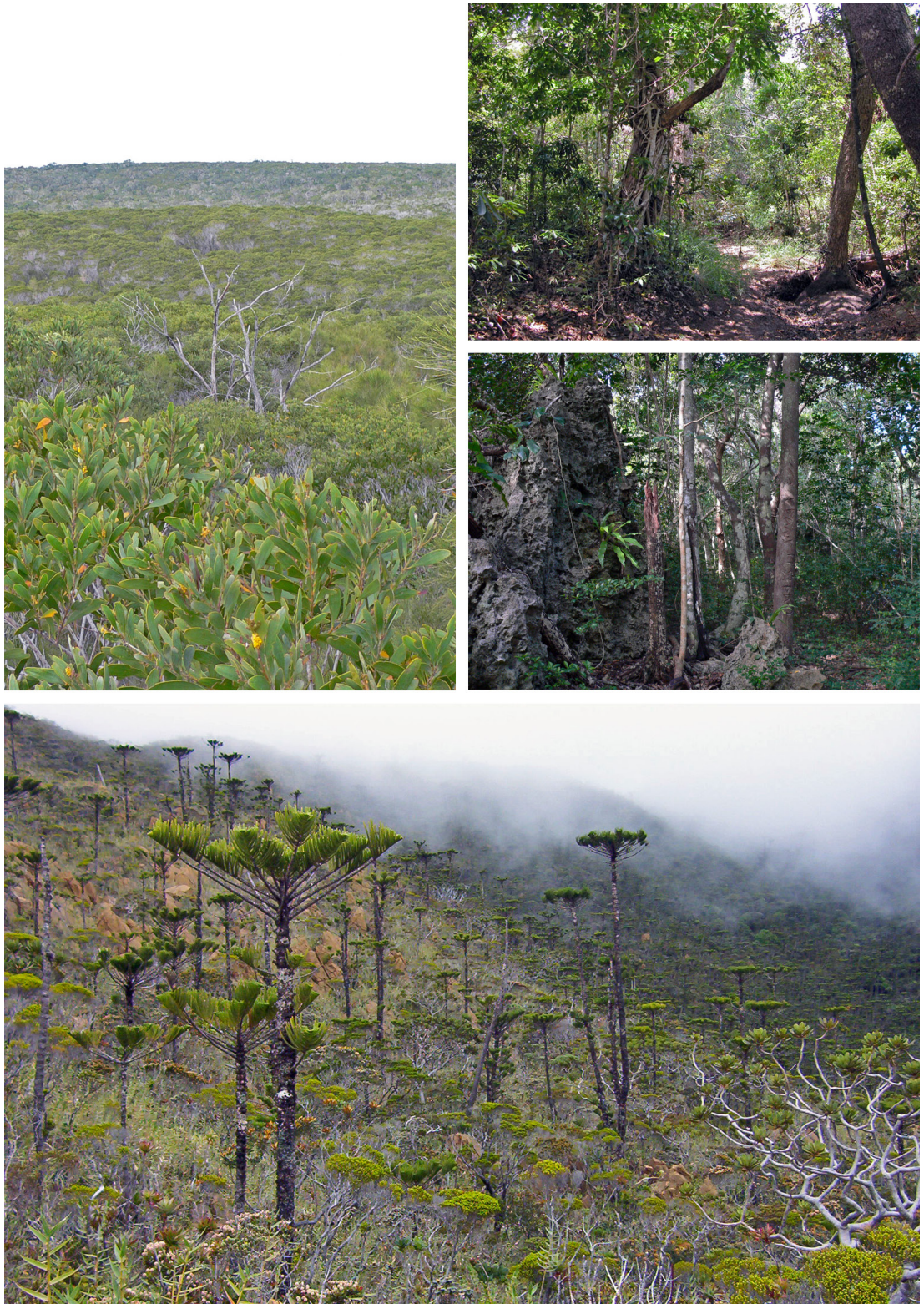


Figure 1.13: Dry sclerophyll forest near Pindai (top left) and Pouembout (top right); rainforest on limestone, Ouvéa (middle right); and high-altitude maquis on Mont Humboldt at 1500-1600 m (bottom). Credit: Jörn Theuerkauf



Figure 1.14: 'Niaouli' savannah at Parc des Grandes Fougères (top left and right*), and near Canala (bottom**).
Credit: Mélusine Lefebvre* & Jörn Theuerkauf**



Figure 1.15: Pine plantations at Parc des Grandes Fougères (top left); mangroves near Hienghène (top right*); and disused coconut plantations near Poindimié (bottom*). Credit: Mélusine Lefebvre*

FAUNAL DIVERSITY

The terrestrial fauna of New Caledonia is very original, yet large gaps remain in our knowledge of certain groups (Chazeau *et al.* 1994). As for most regions of the world, the invertebrate fauna requires further taxonomic study, though it is rich in species. It is estimated that only 4,000 species of insects have been formally described, out of a projected 20,000 (Chazeau 1993, Lowry *et al.* 2004). Insect endemism is high at both specific and generic levels, reaching 100% in the Ephemeroptera and Psocoptera, 80% in the Blattodea, and 70% in Phasmatodea and Dermaptera (Chazeau 1993). There are at least 200 native terrestrial gastropods in New Caledonia, all of which are endemic, and many more remain to be catalogued (Lowry *et al.* 2004). Of the araneomorphs, or 'true spiders', some 194 species (belonging to 112 genera and 33 families) have been recorded in New Caledonia, including many endemics, but numerous species probably await discovery (Platnick 1993). The New Caledonian mainland is perhaps the only island in the world to have an endemic family of spiders, the Bradystichidae (Platnick 1993).

Among the vertebrates, the reptiles stand out for their remarkable diversity and endemism. New Caledonia harbours over 112 indigenous lizard species (95% endemic) belonging to 24 genera (75% endemic) and 3 families (Gekkonidae, Diplodactylidae, and Scincidae) (Whitaker *et al.* 2004). Some of the more novel examples include *Rhacodactylus leachianus*, the largest gecko in existence, and *Phoboscincus bocourti*, one of the largest skinks, which was recorded once around 1870, and not observed again until its rediscovery in 2003 (Ineich 2006, Meiri 2008). When humans first arrived in New Caledonia, the herpetofauna was even more unusual, and included meiolaniid turtles, mekosuchine crocodiles, and varanids (Balouet & Olson 1989, Bauer & Vindum 1990, Chazeau 1993, Whitaker *et al.* 2004). Terrestrial snakes and amphibians appear to be recent introductions (Bauer 1988, Bauer & Vindum 1990, Chazeau 1995). There are nine endemic species of freshwater fish, including a galaxiid, *Galaxias neocaledonicus* (Waters *et al.* 2000, Keith 2002, Lowry *et al.* 2004). The only indigenous land mammals present belong to the Chiroptera, of which six of the nine species are endemic (Lowry *et al.* 2004).

The New Caledonian avifauna is one of the richest and most original in the southwest Pacific (Barré & Dutson 2000). Of the 181 taxa recorded in the region, 112 are indigenous birds that breed locally, and 87 of these are terrestrial (57 endemic and 30 non-endemic). The endemic land birds, comprising 23 species and 34 subspecies (Barré & Dutson 2000, Barré *et al.* 2010), are of greatest interest from a biogeographical and conservation standpoint. The most peculiar of these is the flightless Kagu (*Rhynochetus jubatus*), the sole representative of the Rhynochetidae family (Létocart & Salas 1997). Of the two other endemic genera, *Drepanoptila* is represented by a single species, the Cloven-feathered Dove (*Drepanoptila holosericea*), and *Eunymphicus* is represented by two species, the Horned Parakeet (*Eunymphicus cornutus*), and the Ouvéa Parakeet (*Eunymphicus uvaeensis*).

Several endemic species, namely the New Caledonian Rail (*Gallirallus lafresnayanus*), New Caledonian Owlet-nightjar (*Aegotheles savesi*), and New Caledonian Lorikeet (*Charmosyna diadema*), are only known from a few specimens and a handful of sightings over the past 150 years (Layard & Layard 1881b, Stokes 1979, 1980, Hannecart & Létocart 1983, Balouet & Olson 1989, Ekstrom *et al.* 2002, Tobias & Ekstrom 2002). The same is true of two other endemic taxa, specifically the New Caledonian Painted Buttonquail, *Turnix (varia) novaecaledoniae*, and the New Caledonian White-throated Nightjar, *Eurostopodus (mystacalis) exul*, which may represent distinct species in their own right, but are possibly extinct (Hannecart & Létocart 1983, Balouet & Olson 1989, Ekstrom *et al.* 2002, Tobias & Ekstrom 2002, Anderson *et al.* 2010, Boyer *et al.* 2010).

Other endemic species of conservation interest include the Crow Honeyeater (*Gymnomyza aubryana*), one of New Caledonia's rarest birds, and the 'notou' or New Caledonian Imperial Pigeon (*Ducula goliath*), a large arboreal pigeon that is subject to hunting pressure (Ekstrom *et al.* 2002, Barré *et al.* 2003). From the fossil record, it is evident that at least eleven other non-passerine birds have been extirpated since the arrival of humans in New Caledonia, including a gigantic, flightless galliform, *Sylviornis neocaledoniae*, a very large, flightless swamphen, *Porphyrio kukwiedei*, a large, robust species of megapode, *Megapodius molistructor*, and a large, lowland species of Kagu, *Rhynochetos orarius* (Balouet & Olson 1989).

ORIGINS OF THE NEW CALEDONIAN BIOTA

New Caledonia has a complex geological history, which precludes a simple explanation for the origins of its diverse and highly endemic biota. The mainland has traditionally been viewed as a continental island, with a biota comprised of archaic forms dating back to Gondwanan times, as well as more recent arrivals that have dispersed over water (e.g. Morat 1993b). However, geological evidence points to a long period of submergence during the Paleogene (Pelletier 2007), which has led some authors to suggest that the entire terrestrial biota must have arrived via long-distance dispersal (e.g. Carlquist 1974, Pole 1994). Although many of New Caledonia's species are clearly recent immigrants, the existence of numerous phylogenetic relicts with limited dispersal ability suggests that at least some land must have remained above water during subsidence (Morat *et al.* 1986, Heads 2008, Jolivet & Verma 2008). The remarkable familial and generic diversity of plants would be difficult to explain otherwise (Lowry 1998), as would the presence of several primitive angiosperm families such as the endemic, monotypic Amborellaceae (*Amborella trichopoda*), which is sister to all other extant angiosperms (Zanis *et al.* 2002).

The flora underwent significant changes at the end of the Eocene (Jaffré *et al.* 1987), following the establishment of a sheet of ultramafic rocks over much of the mainland (Chevillotte *et al.* 2006). Those plants that adapted early, or were pre-adapted, to the poor soil conditions associated with the ultramafic substrates probably had a selective advantage over more recent arrivals (Jaffré 1980). Adaptive radiation of these ancestral lineages is partly responsible for the diversity of species that currently occupy the ultramafic massifs, a number of which are tolerant of heavy metals (Jaffré *et al.* 1987). Over time, the fragmentation of the ultramafic mantle promoted further speciation as populations became increasingly isolated (Jaffré *et al.* 1987, Morat 1993a). Many species are now restricted to specific microhabitats that have arisen from the diverse edaphic and climatic conditions on the mainland (Grandcolas *et al.* 2008). However, micro-endemism is not exclusive to plants. Many lizards also have very specific habitat requirements, and their distribution can often be linked to particular vegetation types (e.g. *Rhacodactylus chahoua* is restricted to relatively tall, closed forest), geological substrates (e.g. *Rhacodactylus auriculatus* and *Lioscincus maruia* only occupy ultramafic massifs), or rainfall patterns (e.g. *Marmorosphax tricolor* and *Tropidoscincus boreus* occur at higher elevations along the drier west coast) (Bauer & Vindum 1990, Whitaker *et al.* 2004).

The New Caledonian fauna is composite in nature, comprising both ancient elements that have evolved locally over a long period of time, and more recent colonists

that have originated from a variety of sources (Chazeau 1995). Among the invertebrates with potential Gondwanan affinities are the endemic Troglosironidae, an ancient family of harvestmen that appear to lack the ability to disperse across oceanic barriers (Boyer *et al.* 2007, Sharma & Giribet 2009), and the mygalomorph spiders, which typically have small ranges and high levels of endemism, and are notoriously absent from most oceanic islands on account of their poor dispersal ability (Raven 1980, Platnick 1993). Many invertebrates are highly original and possess archaic characteristics, including the less mobile insects (e.g. Blattodea, Dermaptera, Phasmatodea), gastropods, springtails, as well as certain moths (e.g. Hepialidae, Micropterigidae) and arachnids (e.g. Bradystichidae) (Chazeau *et al.* 1994).

Among the vertebrates, the lizards provide evidence that considerable evolutionary diversification has taken place *in situ* (Bauer & Sadlier 1993). The diplodactyloid geckos have been present in New Caledonia for a very long time, probably arising through vicariance (Bauer & Vindum 1990, Bauer & Sadlier 1993, Oliver & Sanders 2009). Diplodactyloid egg shells are leathery and permeable to saltwater, which likely limits their ability to cross oceans (Bauer 1988, Bauer & Vindum 1990). In comparison, most of the gekkonine geckos, whose egg shells are calcareous and able to withstand exposure to saltwater, probably arrived via dispersal or through human intervention (Bauer 1988, Bauer & Vindum 1990).

Birds are typically seen as poor subjects for studying biogeographical relationships, on account of their vagility. However, not all birds possess the same dispersal ability as others. Furthermore, if we accept that New Caledonia possesses an archaic element in its biota, then it may well extend to the avifauna. Several of the larger birds from the fossil record appear unlikely to have flown to New Caledonia, especially *Sylviornis neocaledoniae*, which stood 1.2-1.6 m tall and weighed around 40 kg (Chazeau 1993, Steadman 1999). For birds like *Sylviornis*, it could be argued that gigantism and flightlessness evolved after dispersal, but this is debatable. Among the extant birds with poor dispersal ability is the flightless Kagu (*Rhynochetus jubatus*), whose closest living relative is the monotypic Sunbittern (*Eurypyga helias*) of the Eurypygidae of South America (Fain & Houde 2004, Ericson *et al.* 2006). Previous land connections through Antarctica might provide an explanation for the present disjunction in their distributions (Cracraft 1982, 2001). Owlet-nightjars (Aegothelidae) maintain a strictly Australasian distribution that ranges from the Moluccas to New Guinea, Australia, and Tasmania, and includes New Caledonia and historically, New Zealand (Dumbacher *et al.* 2003). Despite the fact that

Aegothelidae have not reached any other islands off the Sahul continental shelf, or elsewhere in the Pacific, their presence in New Caledonia and New Zealand has been attributed to dispersal from Australia (Dumbacher *et al.* 2003). An alternative hypothesis, proposed by Heads (2010), is that the New Caledonian Owlet-nightjar (*Aegotheles savesi*), and the extinct New Zealand Owlet-nightjar (*A. novaezealandiae*) were separated from their Australian counterparts as a result of the opening of the Tasman Basin. Elucidating the origin of New Caledonia's parrots is more complicated, as several genera are involved, each with their own unique history. First, however, a description of the New Caledonian parrot fauna is warranted.

PARROTS OF NEW CALEDONIA

DESCRIPTIONS

New Caledonia's parrots can be separated into two distinct tribes: Platycercini (broad-tailed parrots), and Loriini (lorikeets) (Smith 1975, Mayr 2008). The 'broad-tailed' parrots, or platycercines, have a robust beak, and are mainly granivorous, whereas the lorikeets have a relatively thin, elongated beak, and a brush-tipped tongue for harvesting pollen and nectar (Delacour 1966, Forshaw 1989). The New Caledonian Parakeet (*Cyanoramphus saisseti*), Horned Parakeet (*Eunymphicus cornutus*), and Ouvéa Parakeet (*E. cornutus*) all belong to the Platycercini, while the New Caledonian Lorikeet (*Charmosyna diadema*) and New Caledonian Rainbow Lorikeet (*Trichoglossus haematodus deplanckii*) both belong to the Loriini.

CYANORAMPHUS

Cyanoramphus parakeets are stocky, small to medium-sized birds with long, gradated tails (Forshaw 1989). They are predominantly green in colour, with a small amount of blue on their wings. Some of the *Cyanoramphus* parakeets have red, orange or yellow patches on their head and rump (Taylor 1975). Females are smaller than males, but their plumage is similar (Forshaw 1989). Parakeets of the *Cyanoramphus* genus have adapted to a variety of different habitats ranging from tropical rainforests to subantarctic tussock grasslands (Chambers *et al.* 2001). They are distributed throughout the islands of the southwest Pacific (Figure 1.4), including mainland New Caledonia, Norfolk Island, New Zealand (and adjacent islands), Kermadec Islands, Chatham Islands, and Antipodes Island. *Cyanoramphus* parakeets once existed on Lord Howe Island, Macquarie Island, and the

Society Islands, but these taxa have become extinct since European settlement (Taylor 1985, Boon *et al.* 2001). At present, 8 extant species of *Cyanoramphus* are recognised, including the polytypic *C. novaezelandiae*, and 3 species and 1 subspecies have gone extinct (Boon *et al.* 2001, Chambers & Boon 2005).

***Cyanoramphus saisseti* – New Caledonian Parakeet**

Verreaux & des Murs, 1860

Cyanoramphus saisseti (Figure 1.16) is a mid-sized (26-32 cm) parrot with a long (13-17 cm), graduated tail (Verreaux & des Murs 1860, Salvadori 1891, Delacour 1966, Hannecart & Létocart 1980, Forshaw 1989, Juniper & Parr 1998, Doughty *et al.* 1999). The upperparts are mostly green, with some bluish-green on the tail, violet-blue along the outer webs of the flight feathers, and patches of red on either side of the rump. The underparts are yellowish-green, yellower near the throat, and grey under the tail (Forshaw 1989, Juniper & Parr 1998, Doughty *et al.* 1999). A patch of red extends from the crown to the forehead, and runs in a thin band from the forehead back to the ear coverts (Juniper & Parr 1998). The bill is leaden grey, tipped with black, the irises are red-orange, and the legs are dark grey (Layard & Layard 1882b, Juniper & Parr 1998). Males typically exceed females in size, though their plumage is similar (Verreaux & des Murs 1860, Layard & Layard 1882b, Salvadori 1891, Forshaw 1989). The New Caledonian species can be distinguished from other *Cyanoramphus* taxa by its distinctive yellowish-green undersurface and its slightly larger size (Layard & Layard 1882b, Salvadori 1891, Forshaw 1989, Juniper & Parr 1998).

Most authors describe the New Caledonian Parakeet as a forest species (e.g. Layard & Layard 1882b, Delacour 1966, Hannecart & Létocart 1980), inhabiting either dense primary forests (Doughty *et al.* 1999), or indigenous mountain forests (Taylor 1985, Juniper & Parr 1998). The species has also been observed in maquis (Hannecart & Létocart 1980, Barré & Dutson 2000, Ekstrom *et al.* 2000, 2002), in addition to savannah, and high-altitude rainforests (Barré & Dutson 2000). To date, however, no attempt has been made to quantify the use of different habitats. The species reportedly feeds in the lower or middle storey (Forshaw 1973, Juniper & Parr 1998), but has also been observed feeding on the ground (Layard & Layard 1882b, Delacour 1966, Juniper & Parr 1998). It is essentially granivorous (Delacour 1966), feeding mainly upon seeds and fruits (Hannecart & Létocart 1980), in addition to berries, nuts, and various other plant parts (buds, blossoms, leaves, etc.) (Forshaw 1989). Although these parakeets are not particularly timid, they tend to be rather quiet and difficult to observe (Hannecart & Létocart 1980, Juniper & Parr 1998).



Figure 1.16: Photograph of the New Caledonian Parakeet (*Cyanoramphus saisseti*).

The New Caledonian Parakeet is endemic to the main island of New Caledonia, though uncertainties remain over the extent of its range, and the size of its population (Taylor 1985, Juniper & Parr 1998). The species was considered rare at the time of its description (Verreaux & des Murs 1860). However, in the 1880s, flocks of birds were reported in the west, flying into the valleys at Moindou from the mountain forests nearby, where they are rumoured to have roosted in large numbers (Layard & Layard 1882b). In

1911-1912, an expedition by Sarasin (1913) failed to obtain any specimens, which suggests that the species was probably already scarce by then, or at least localised (Bregulla 1993). In the 1930s, the species was recorded from the northwest, though it was apparently not very common there (Forshaw 1989). Berlioz (1945) was unable to provide much information about the status of the species, except to suggest that it probably persisted in the mountainous areas that were rarely visited. Likewise, Orenstein (1972) considered the species to be relatively common in undisturbed regions, attributing its continued existence to the presence of forest. In 1974, during about two weeks of field work covering a variety of habitats, Vuilleumier & Gochfeld (1976) encountered the species only once or twice, in lowland forest near Lake Yaté. In 1975, another individual was located above La Coulée, near Mont Dore (Forshaw 1989). During a month-long search for the New Caledonian Rail (*Gallirallus lafresnayanus*), Stokes (1980) observed *C. saisseti* only once, feeding quietly in the rainforest near the Rivière Bleue/Rivière Blanche, but recorded no observations from Mont Panié or the headwaters of the Ouinné River. Bregulla (1993) considered the New Caledonian Parakeet to have the lowest population density of the New Caledonian parrots that are known to still exist.

Juniper & Parr (1998) drew attention to the lack of observer coverage on the island, and suggested that the species may still be fairly common in undisturbed areas. Doughty *et al.* (1999) stated that the species could be found throughout the island in intact forests, but acknowledged that recent sightings were mainly from the south. They described the species as being uncommon, localised, and in decline. Ekstrom *et al.* (2000, 2002) recorded the species as being present (uncommon to fairly common) at seven of the nine rainforest sites visited during field work in 1998, and also observed the species in small patches of scrubby forest within a maquis landscape. They concluded that the species was relatively widespread, but only occurred at low densities. On account of the species' precarious status, it is considered 'vulnerable' by the IUCN (2011).

New Caledonian Parakeets are typically observed in small numbers, either travelling alone, in pairs, or in small flocks presumably comprised of family members (Layard & Layard 1882b, Delacour 1966, Juniper & Parr 1998). Nesting is reported to occur between November and January, and clutches consist of two to five eggs, which are laid in a tree hollow (Hannecart & Létocart 1980, Theuerkauf *et al.* 2009b). Genetic evidence indicates that the species is polyandrous, and the presence of male feeding helpers suggests that the mating system probably involves cooperative polyandry (Theuerkauf *et al.* 2009b). There are no indications of widespread nest poaching, although two parakeets

were reportedly taken from a nest of three during the 2004/2005 breeding season, apparently from an unprotected area (Pain *et al.* 2006).

EUNYMPHICUS

Eunymphicus parakeets bear some resemblance to *Cyanoramphus* parakeets, in that they are mostly green, with yellowish-green underparts, and have blue along the edge of their wings (Forshaw 1989, Juniper & Parr 1998). However, the genus is easily recognised by its peculiar coronal 'crest', formed from several elongated crown feathers (Forshaw 1989).

Eunymphicus parakeets also have a dark face patch, which is absent in *Cyanoramphus* (Juniper & Parr 1998). The genus is endemic to New Caledonia, and consists of only two species: *E. cornutus* from the main island, and *E. uvaensis* from Ouvéa (Juniper & Parr 1998, Boon *et al.* 2008).

***Eunymphicus cornutus* - Horned Parakeet**

(Gmelin, 1788)

Eunymphicus cornutus (Figure 1.17) is a fairly large (30-36 cm) parrot with a long (14-18 cm) tail (Jouan 1863, Layard & Layard 1882b, Delacour 1966, Hannecart & Létocart 1983, Forshaw 1989, Bregulla 1993, Juniper & Parr 1998, Doughty *et al.* 1999). The plumage is predominantly green above, and tinged with violet-blue towards the tip of the tail and the outer webs of the primaries (Forshaw 1989, Juniper & Parr 1998). The underparts are of a paler, yellowish-green, and the underside of the tail is grey (Juniper & Parr 1998). The hind crown, nape, and ear coverts are golden yellow, fading to yellowish-green below the cheeks (Salvadori 1891, Juniper & Parr 1998). The face is black from the chin to the lores, and back to the rear of the eyes (Salvadori 1891). A scarlet cap covers the forehead and forepart of the crown (Forshaw 1989). From the middle of the crown spring two slender black feathers, about 4-8 cm in length, and tipped with crimson (Latham 1781, Jouan 1863, Layard & Layard 1882a, Bregulla 1993, Boon *et al.* 2008). The irises are orange-red, the bill is bluish-grey at the base, deepening to black at the tip, and the legs are dark grey (Latham 1781, Layard & Layard 1882b, Delacour 1966, Forshaw 1989). In juveniles, the crown is darker, the hind neck and ear coverts are greenish-yellow, and the bill resembles aged ivory (Salvadori 1891, Forshaw 1989). There are no colour differences between males and females, although males are generally slightly larger, especially their head and bill, and their crest is usually wider and longer (Layard & Layard 1882b, Bregulla 1993, Boon *et al.* 2008). In the early descriptions of the New Caledonian avifauna, there is mention of a 'Caledonian Parrot', which was placed the same genus as the Horned Parakeet (*i.e.* *Psittacus*, and later

Platycercus), and was suspected of being either the female, or the immature form of the Horned Parakeet on account of similarities in the bill, legs, wings, and tail (Latham 1781, Gmelin 1788, Gray 1859, Layard & Layard 1878, Oustalet 1879, Tristram 1879, Sarasin 1913). As it turns out, however, the original description was of a Green Rosella collected from Tasmania, which explains why this endemic Tasmanian parrot has been given the unusual name of '*Platycercus caledonicus*' (Stresemann 1950).

The number of Horned Parakeets appears to have declined since 1882, when they were believed to occur in all forested regions of the mainland (Layard & Layard 1882b). Berlioz (1945) reported them to be fairly abundant in all the wooded areas of the island, at both low and high altitudes, and felt that there was no need for concern, given their relative abundance. On the contrary, Warner (1947) only found them to be reasonably common in less accessible regions above 470 m (in Forshaw 1989). Delacour (1966) felt that the species was still fairly widespread in rainforests, and Orenstein (1972) judged them to be relatively common in undisturbed regions, particularly where *Araucaria* and *Agathis* trees were present. However, Vincent (1967) pointed out that their habitat requirements were somewhat specialised and believed that their populations were low enough to raise concern. During field work from 1962 to 1964 and from 1976 to 1980, Bregulla (1993) regularly encountered Horned Parakeets in suitable habitat, though they were apparently not very abundant. Bregulla (1993) considered rainforest to be the principal habitat of this species, but also reported them from secondary forests and wooded savannah, and observed them foraging in maquis. According to Hahn (1993), the population of Horned Parakeets declined considerably from 1977 to 1993. In the year 2000, the population was roughly estimated at 2,000 individuals (Barré & Dutson 2000), although recent surveys suggest that this is likely to be an underestimate (Chartendrault & Barré 2005, 2006). Given its small population size, the Horned Parakeet is listed as 'vulnerable' by the IUCN (2011).



Figure 1.17: Photograph of the Horned Parakeet (*Eunymphicus cornutus*).

Ekstrom *et al.* (2000, 2002) generally found Horned Parakeets to be most common at sites dominated by rainforest with a canopy of 10 to 30 m. These authors considered the distribution of the species to be patchy, and concentrated mainly in the forests on ultramafic soil in the southern half of the mainland. They concluded, however, that the species must have more specific habitat requirements because it was not present at all of the ultramafic forest sites in the south. Various authors, including Ekstrom *et al.* (2000, 2002), have recorded Horned Parakeets in the vicinity of the Rivière Bleue, in the

Southern Province (e.g. Delacour 1966, Orenstein 1972, Hannecart & Létocart 1983).

Stokes (1980) viewed this area as the last stronghold for the species, and recent accounts suggest that the local population of Horned Parakeets is relatively stable there (Ekstrom *et al.* 2000). However, several other sites are likely to be of similar importance for the conservation of Horned Parakeets, including Nodela, Col d'Amieu, Néoua, and Forêt Plate (Hannecart & Létocart 1983, Barré & Dutson 2000, Ekstrom *et al.* 2000, 2002).

Horned Parakeets feed on the seeds, fruits, berries, nuts, and flowers of a variety of trees and shrubs, including the cones of *Agathis lanceolata*, the fruit of *Carica papaya*, the seeds of *Flindersia fourneri*, the kernels of *Aleurites moluccana*, and the blossoms of *Erythrina* (Layard & Layard 1882b, Delacour 1966, Hannecart & Létocart 1983, Forshaw 1989, Doughty *et al.* 1999, Ekstrom *et al.* 2000). They have been observed feeding on the ground, but this is uncommon (Layard & Layard 1882b). When feeding, the Horned Parakeet often chuckles quietly to itself, before announcing its departure with a series of loud honks. At times, they can be rather noisy, and are usually detected by ear rather than by sight (Delacour 1966, Juniper & Parr 1998). Their vocalisations generally have a nasal tone, and the typical call is described by Forshaw (1989) as a raucous 'ko-kot...ko-kot'. Horned Parakeets are usually observed in pairs or small groups perching in the tops of tall trees (Hannecart & Létocart 1983, Forshaw 1989). These parrots typically travel short distances, and their flight is swift and slightly undulating (Hannecart & Létocart 1983, Forshaw 1989).

Horned Parakeets nest in the hollow trunks or limbs of living trees, as well as in cavities among rocks, and in hollowed-out trees on the ground (Layard & Layard 1882b, Delacour 1966, Hannecart & Létocart 1983, Forshaw 1989, Hahn 1993, Barré & Dutson 2000). Nesting takes place from September to January, and a clutch usually contains two to four eggs (Layard & Layard 1882b, Hannecart & Létocart 1983, Forshaw 1989, Hahn 1993, Theuerkauf *et al.* 2009b). Nests are usually occupied by a single couple, although nest sharing has also been observed on rare occasions (Hahn 1993, Theuerkauf *et al.* 2009b).

***Eunymphicus uvaeensis* - Ouvéa Parakeet**

(Layard & Layard, 1882)

The Ouvéa Parakeet (Figure 1.18) was previously treated as a subspecies of *Eunymphicus cornutus*, but it seems to be sufficiently distinct to warrant full species status (Juniper & Parr 1998, Boon *et al.* 2008). It is fairly similar in size and shape to the Horned Parakeet, though the latter is a little bigger on average (Layard & Layard 1882a, Barré & Dutson 2000, Boon *et al.* 2008). The Ouvéa Parakeet is, nevertheless, a relatively large (32-36

cm) parrot, with a fairly long (14-16 cm) tail (Salvadori 1891, Hannecart & Létocart 1983, Forshaw 1989, Juniper & Parr 1998, Barré & Dutson 2000). As observed in the Horned Parakeet, the plumage is mainly green above, and yellowish-green below (Salvadori 1891, Juniper & Parr 1998). The upperside of the tail is green, becoming bluish near the tip, and the underside of the tail is grey (Salvadori 1891, Juniper & Parr 1998). The outer webs of the primaries are greenish-blue, similar to the Horned Parakeet, but of a less brilliant blue (Layard & Layard 1882a, Juniper & Parr 1998). Unlike the Horned Parakeet, there is no yellow on the head, and the hind neck, ear coverts, and cheeks are green (Layard & Layard 1882a, Salvadori 1891, Forshaw 1989). The face of the Ouvéa Parakeet is dark green, instead of black, and the scarlet cap is greatly reduced, occupying only the centre of the forehead (Layard & Layard 1882a, Forshaw 1989). At close range, the most noticeable difference is the crest (Figure 1.19), which, in the Ouvéa Parakeet, is formed of six upturned green feathers, about 3-4 cm in length (Layard & Layard 1882a, Boon *et al.* 2008). It seems that, in both of these species, the exact number of crest feathers may vary slightly, presumably due to feather turnover (Layard & Layard 1882a, Boon *et al.* 2008). Similar to the Horned Parakeet, the irises are reddish-orange, the base of the bill is blue-grey, tipped in black, and the legs are dark grey (Salvadori 1891, Juniper & Parr 1998). Females resemble males, but are slightly smaller (Salvadori 1891, Forshaw 1989, Boon *et al.* 2008).

The Ouvéa Parakeet is endemic to the small (130 km²), flat (less than 50 m a.s.l.) island of Ouvéa, which comprises part of the Loyalty Archipelago (Barré *et al.* 2010). The species was once distributed in forests throughout the island, yet these have been greatly reduced, partly from bushfires in the 1930s, which eliminated most of the parakeet's habitat in the south, but also from clearing for coconut plantations and subsistence crops, and from the felling of trees for firewood and construction (Hannecart & Létocart 1983, Robinet 1997, Barré & Dutson 2000, Robinet *et al.* 2003). The Ouvéa Parakeet now mainly occurs in the relatively undisturbed patches of forests in the northern part of the island, which are comprised of medium to tall trees, about 10 to 15 m high (Robinet 1997, Robinet *et al.* 2003, Barré *et al.* 2006, 2010).



Figure 1.18: Photograph of the Ouvéa Parakeet (*Eunymphicus uvaeensis*). Credit: Jörn Theuerkauf

Parakeets have traditionally been captured and kept as pets on Ouvéa (Robinet 1997). However, this practice has intensified in the past century in order to meet external demand by collectors (Sarasin 1913). The exportation of Ouvéa Parakeets has probably never been sustainable, and their population has presumably been in decline since it began (Sarasin 1913, Berlioz 1945, Robinet 1997). In the 1940s, the population was roughly estimated at 1,000 birds (Warner 1947, in Robinet 1997). In 1963, 15 parakeets were transferred to the larger, more densely forested island of Lifou, but this failed to establish a second population (Delacour 1966, Robinet 1997, Barré *et al.* 2010). There are anecdotal reports of an earlier attempt to introduce 100 birds to Lifou in 1925, but this was also unsuccessful, if it occurred at all (Delacour 1966, Robinet 1997). In 1977, the Ouvéa Parakeet population was estimated to comprise 500 to 800 individuals, based on extrapolations from nest counts (Robinet 1997). However, other authors suggested that fewer than 200 individuals remained (King 1981, Lambert *et al.* 1993), perhaps even fewer than 100 (Hahn 1993). In 1993, fixed distance line transects revealed a total population of 617 (274-996) birds (Robinet *et al.* 1996). Around this time, it was estimated that at least 30 to 50 young were being captured per year, despite this being strictly prohibited by law (Robinet *et al.* 1996).

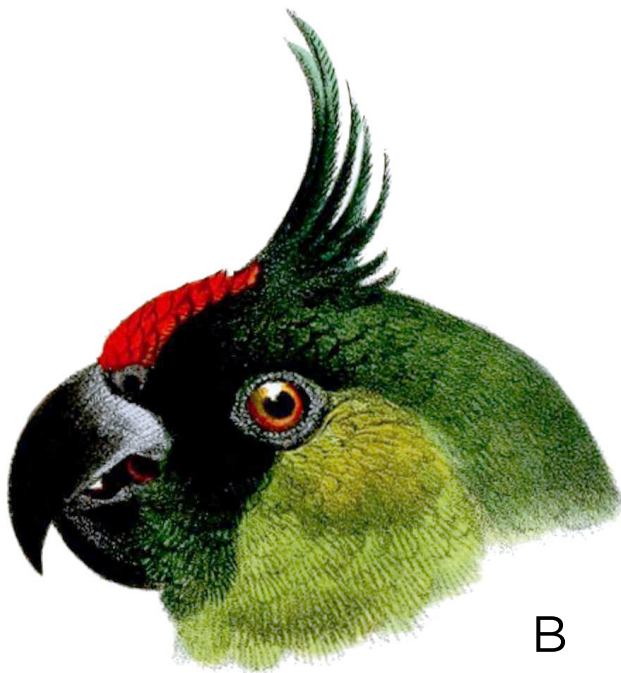


Figure 1.19: Illustrations showing the main morphological differences between (A) *Eunymphicus cornutus* and (B) *Eunymphicus uvaeensis* (Layard & Layard 1882a).

Since 1992, measures have been taken to prevent the extinction of the Ouvéa Parakeet, such as employing local guides, protecting and restoring existing nests, providing artificial nests, and raising public awareness (Robinet 1997, Robinet *et al.* 2003, Barré *et al.* 2010). Although the artificial nest box trials were unsuccessful, the remaining measures appear to have effectively reversed the decline, as the density of parakeets on Ouvéa has increased considerably since their implementation (Barré *et al.* 2010). Hiring local members of the community as guides appears to have been integral to the process, as their presence essentially eliminated nest poaching (Barré *et al.* 2010). As a result, the density of Ouvéa Parakeets has increased, and the population was estimated at 2,090 (1,280-3,413) birds in 2009 (Barré *et al.* 2010).

Ouvéa Parakeets are often observed foraging in small forest gardens (Robinet 1997, Barré & Dutson 2000, Barré *et al.* 2006). It is perhaps no surprise that the species can be found in such environments, given their close proximity to forest, and their continual supply of food. One of their favourite foods is pawpaw (*Carica papaya*), an introduced cultivar that is preferred during the latter half of the breeding season, from November onwards (Robinet 1997). Ouvéa Parakeets also forage upon a wide variety of native species throughout the year (Robinet 1997, Robinet *et al.* 2003). *Ficus* species are particularly favoured, and appear to be a key source of food from May to October, leading up to the breeding season (Robinet *et al.* 2003).

The breeding season of the Ouvéa Parakeet is longer than that of the Horned Parakeet. It stretches from July/August until late January, and second clutches are known to occur (Robinet & Salas 1999). Nesting takes place in hollow trunks or branches, mainly in large *Syzygium* or *Mimusops* trees (Hahn 1993, Robinet & Salas 1999, Robinet *et al.* 2003). Parakeets exhibit strong site attachment during the breeding season, and return to the same nest sites in consecutive years (Robinet & Salas 1999, Robinet *et al.* 2003). The average clutch size is 2.9 eggs (ranging from 2 to 4), and the hatching success rate is about 90% (Robinet & Salas 1999). The male supplies the female with food, while she incubates the eggs and broods the nestlings. Initially, the young are only fed by the female, but after about two weeks of hatching, they begin to receive food from the male as well (Robinet & Salas 1999). There are no indications of cooperative breeding in this species (Robinet & Salas 1999, Theuerkauf *et al.* 2009b). The main factors contributing to the loss of parakeets include starvation of the youngest chicks, poaching of hatchlings, and predation of fledglings, especially by raptors (Robinet & Salas 1999). Nest predation is relatively uncommon, presumably due to the absence of Black Rats (*Rattus rattus*) on

Ouvéa (Robinet & Salas 1999). Previous attempts to establish a population of Ouvéa Parakeets on Lifou may have failed due to predation by Black Rats (Delacour 1966, Robinet 1997, Robinet *et al.* 1998).

TRICHOGLOSSUS

Lorikeets of the genus *Trichoglossus* are small to medium-sized birds with orange bills and gradated tail feathers. These parrots often have brilliantly coloured, glossy plumage, and barring is often observed on the breast (Forshaw 1989). The generic name is in reference to their tongue, which is tipped with elongated papillae to assist with the harvesting of pollen and nectar (*'tricho'* = *'hair'*; *'glossus'* = *'tongue'*) (Higgins 1999). Males and females resemble one another, and form long-term bonds as adults (Serpell 1981). *Trichoglossus* parrots display elaborate visual and vocal signalling behaviour, and are unusually hostile towards other birds with respect to food, perches, and nests (Serpell 1981, 1982). Members of this genus are believed to be nomadic or semi-nomadic (Serpell 1981). *Trichoglossus* parrots are widely distributed across Indonesia, New Guinea, coastal Australia, and many of the islands in the south Pacific (Serpell 1989). A total of seven species are currently recognised, including the Rainbow Lorikeet (*T. haematodus*), which is the most widespread by far, and comprises up to 20 different subspecies (Forshaw 2010).

***Trichoglossus haematodus deplanckii* - New Caledonian Rainbow Lorikeet**

Verreaux & des Murs, 1860

The New Caledonian Rainbow Lorikeet (Figure 1.20) is a midsized (24-28 cm), slender parrot with a relatively long (12-13 cm), tapered tail (Verreaux & des Murs 1860, Jouan 1863, Layard & Layard 1882b, Berlioz 1945, Delacour 1966, Hannecart & Létocart 1980, Bregulla 1993). The crown, cheeks and chin are streaked in blue, and the back is predominantly green, fading to yellowish-green at the nape, and stained with patches of red on the hind neck (Verreaux & des Murs 1860, Jouan 1863, Delacour 1966). The top of the wings and tail are also green, whereas the underside of the wings are coloured red, yellow, and black, and the underside of the tail is yellow (Delacour 1966). The chest and upper abdomen are crimson with black striations, while the lower abdomen and thighs are mottled green and yellow (Jouan 1863, Delacour 1966). The bill is orange, lightening to yellow-orange at the tip, the irises are orange, and the legs are dark grey (Verreaux & des Murs 1860, Layard & Layard 1882b, Delacour 1966). Slight colour differences are apparent between individuals, and immature birds tend to be less vivid than adults. However, females generally resemble males, apart from being slightly smaller (Verreaux & des Murs

1860, Jouan 1863, Tristram 1879, Layard & Layard 1882b, Hannecart & Létocart 1980).

The New Caledonian subspecies differs from its nearest relative, *T. h. massena* (distributed from Vanuatu to the Bismarck Archipelago), mainly by having stronger barring on its chest, and more prominent blue streaking on its face (Forshaw 2010).



Figure 1.20: Photograph of New Caledonian Rainbow Lorikeets (*Trichoglossus haematodus deplanchii*) feeding on pawpaw. Credit: Thorsten Müller

The Rainbow Lorikeet is undoubtedly the most common and widespread parrot on the main island of New Caledonia, and has been for some time (Layard & Layard 1882b, Sarasin 1913, Berlioz 1945, Bregulla 1993, Barré & Dutson 2000). There is little information about its status on the Loyalty Islands, although it appears to be relatively uncommon there, and possibly only exists on Ouvéa, where it was introduced from the mainland in the 1970s (Barré & Dutson 2000, Barré *et al.* 2006). It was historically known to occur on Lifou, but apparently not on Maré (Tristram 1879, Layard & Layard 1880). In general, this species can be found wherever there are flowering trees, especially in savannah, but also in

plantations, mangroves, coconut groves, forests, as well as in villages and towns (Sarasin 1913, Delacour 1966, Vuilleumier & Gochfeld 1976, Stokes 1980, Bregulla 1993, Barré & Dutson 2000, Barré *et al.* 2006). Rainbow Lorikeets travel about swiftly in large, noisy flocks in search of food, and their diet consists largely of pollen and nectar from the flowers of various plants (Sarasin 1913, Delacour 1966, Bregulla 1993). They are particularly fond of blossoming *Melaleuca* and *Erythrina* trees, but also feed upon ripe fruits (e.g. oranges, tangerines, papaya, and banana) (Jouan 1863, Layard & Layard 1882b, Delacour 1966, Bregulla 1993). Rainbow Lorikeets have a wide range of vocalisations, but they are typically recognised by their loud, shrill contact calls (Layard & Layard 1882b, Bregulla 1993). The nesting period spans from around May to July and from around November to January (Hannecart & Létocart 1980, Bregulla 1993). The female lays between two and four eggs in a tree hollow, and is presumably the sole incubator, although the male also spends time in the nest cavity and helps to feed the young (Hannecart & Létocart 1980, Bregulla 1993).

CHARMOSYNA

Charmosyna lorikeets are relatively small parrots with slender tails. The bill is finely pointed, and coloured reddish-orange in most cases. They bear a resemblance to *Vini* lorikeets, but are less stocky and their tails are more gradated. Sexual dimorphism is present in most species, and juveniles resemble females (Forshaw 1989, 2010). This genus is comprised of 14 species, which are distributed from the Moluccas to Papua New Guinea, Solomon Islands, Vanuatu, Fiji and New Caledonia (Forshaw 2010).

***Charmosyna diadema* - New Caledonian Lorikeet**

(Verreaux & des Murs, 1860)

Charmosyna diadema (Figure 1.21) is known only from the type specimen, upon which the following description is based. It is a relatively small (~20 cm), slender lorikeet with a strongly gradated tail of moderate (~9 cm) length, and very pointed wings (Verreaux & des Murs 1860, Doughty *et al.* 1999). The plumage is mostly green; lighter on the forehead, sides of the neck, and underparts, and darker elsewhere, especially on the mantle, primaries, and tail feathers, which end in a greenish-yellow (Verreaux & des Murs 1860). The cheeks, throat, and abdomen are coloured yellow, as well as the underside of the tail, which has some red and black at the base of the lateral feathers (Verreaux & des Murs 1860, Delacour 1966, Forshaw 1989). There is a red patch by the vent, and the crown is azure blue (Verreaux & des Murs 1860). The long, arched, and pointed bill is orange-red, darkening near the tip, and the legs are of similar colour (Verreaux & des Murs 1860,

Forshaw 1989). Verreaux & des Murs (1860) considered the type specimen to be a mature, adult female, and presumed that the yellow on the cheeks, throat, and abdomen might be replaced by bright red in the male, as seen in related species (Delacour 1966). The type specimen is kept at the Museum of Natural History in Paris (Hannecart & Létocart 1983).

Verreaux & des Murs (1860) based their description on a single female specimen, and early reports consistently support the notion that only one specimen of this species was ever preserved (Oustalet 1879, Layard & Layard 1882b, Sarasin 1913, Berlioz 1945, Delacour 1966, Orenstein 1972). Sarasin (1913) apparently procured a second specimen of this species in 1911, which came from the mountains near Oubatche. It was badly damaged, however, and decaying by the time it reached him, thus it was not preserved. In fact, it was in such a poor state that Sarasin was unable to state with certainty that it was *Charmosyna diadema*. Stokes (1980) wrote that two specimens were collected in 1859, but there seems to be no previous mention of this in the literature. It seems plausible that the second specimen that Stokes referred to was actually the one collected by Sarasin. Forshaw (1989) also mentions that two (female) specimens were collected before 1860, but states that one has apparently been lost. Again, the lost specimen was probably the one discarded by Sarasin. In spite of this, most authors have reiterated Stokes (1980) and Forshaw (1989) in recent years, referring to the existence of two specimens collected before 1860 (Collar *et al.* 1994, Juniper & Parr 1998, Doughty *et al.* 1999, Snyder *et al.* 2000), often in addition to the specimen collected by Sarasin (Barré & Dutson 2000, Ekstrom *et al.* 2000, 2002).



Figure 1.21: Illustration of the New Caledonian Lorikeet (*Charmosyna diadema*), by John Gerard Keulemans (1896).

Verreaux & des Murs (1860) provide no information about the location where the type specimen was obtained. This is unfortunate as it was the first and only time that the species was recorded with absolute certainty. Nevertheless, reports of the species existence have circulated since its discovery. In describing the parrots of New Caledonia, Jouan (1863) recalls hearing of a colourful red and green parrot with a crest, which was collected by locals in the interior mountains and sold in Canala. It was the only time he had heard of such a bird, and could hardly believe it existed. A young friend of the Layards (1881a), one who collected for them, reported seeing several small green parrots in the

mountain ranges near Moindou, and described them as being similar to *Charmosyna palmarum* in size and colour. The Layards (1882b) considered *Charmosyna diadema* to be extremely rare. They never observed the species themselves, in spite of considerable effort, but it was known to their friends, the Boyers, as an inhabitant of forested areas. The specimen recorded by Sarasin (1913) would likely have originated from Mont Ignambi, in the far north of the island. When shown a painting of the species (from Delacour 1966), a local with an interest in natural history reported spending several minutes observing a single bird many years ago, perhaps in the 1920s (Stokes 1980, Forshaw 1989). The observation apparently took place in low scrubland near Lake Yaté (Forshaw 1989), though Stokes (1980) referred to the location as being near Plum, about 30 km away by road. In 1953 or 1954, a senior forestry officer claimed to have seen a pair flying from rainforest to wooded savannah along the road from La Foa to Canala (Forshaw 1989). He was familiar with other local species, and remembered the birds being mainly green with yellow on the abdomen. The same individual recalled another encounter with the species that occurred in June 1976, also at the boundary between wooded savannah and rainforest, but this time to the west of Mont Panié (Stokes 1980, Forshaw 1989). This experienced forester noticed two small green parrots alight from a tree, after being drawn to a call that differed slightly from that of the Rainbow Lorikeet. In an interview with Ekstrom *et al.* (2002), a forest warden recalled seeing a small parrot, apparently of this species, near Aoupinié in the 1960s. He reported another observation from the 1960s that took place around the Bokoua forest region near Néoua (Ekstrom *et al.* 2000, 2002).

Several of the *Charmosyna* lorikeets are difficult to detect on account of their small size and predominantly green plumage (Forshaw 1989). They are inconspicuous once settled in the forest canopy, and are more likely to be noticed in flight, or by their calls (Forshaw 1989). Sightings of certain species (e.g. *C. toxopei*, *C. palmarum*, *C. amabilis*) are exceptionally uncommon (Ekstrom *et al.* 2000). The call of *C. diadema* is unknown, though it is supposedly somewhat similar to that of the Rainbow Lorikeet (Stokes 1980, Forshaw 1989). *Charmosyna* lorikeets typically emit high-pitched screeches or squeaks while feeding or in flight, and closely-related species tend to form small, nomadic flocks, flying between flowering trees to feed on nectar and pollen (Forshaw 1989, Bregulla 1992, Ekstrom *et al.* 2000). *C. diadema* is known to have occasionally visited *Erythrina* trees (Layard & Layard 1882b), and the species could potentially be attracted to flowering *Cunonia* or *Metrosideros* plants in the highlands (Bregulla 1993). Some *Charmosyna* species (e.g. *C. amabilis*, *C. palmarum*) are most common in upland rainforests (Forshaw 1989,

Bregulla 1992), and this seems to be the habitat where *C. diadema* is most likely to be found (Juniper & Parr 1998, Ekstrom *et al.* 2000). Bregulla (1993) suggested that searches be carried out in mountainous regions, specifically Mont Panié, Mont Humboldt, and Mont Kouakoué. No records of the species were obtained during 30 days of surveys in the forests of the northeast ranges, including Mont Ignambi (Ekstrom *et al.* 2000, 2002). However, given the size of the island and the amount of rainforest that remains largely unexplored, the species may still exist in relatively undisturbed regions (Juniper & Parr 1998, Ekstrom *et al.* 2000, 2002).

The New Caledonian Lorikeet is clearly a very rare bird, if not already extinct. Its decline could have been due to a number of different factors, including rat predation, avian malaria, or habitat loss. The Pacific Rat (*Rattus exulans*) has been present in New Caledonia since 900 B.C. (Atkinson 1985), and could have contributed to the disappearance of the New Caledonian Lorikeet (Ekstrom *et al.* 2002). However, given that the two species coexisted for such a long period beforehand, it seems rather coincidental that the New Caledonian Lorikeet disappeared so recently. Norway Rats (*Rattus norvegicus*) and Black Rats (*Rattus rattus*) were apparently introduced around 1850 (Atkinson 1985, Gargominy *et al.* 1996). Norway Rats are uncommon in forest (Warner 1948, Nicholson & Warner 1953, Rouys & Theuerkauf 2003), and usually prey upon ground nests because they are not agile climbers (Atkinson 1973, 1985). As a result, they probably pose a relatively minor threat to the New Caledonian Lorikeet, if it still exists. Black Rats appear to have been responsible for the decline of a number of *Charmosyna* and *Vini* lorikeets in the South Pacific (e.g. Seitre & Seitre 1992, Watling 1995), and may have delivered the 'coup de grâce' to the New Caledonian Lorikeet. However, all indications suggest that the New Caledonian Lorikeet was already very scarce at the time of its initial description (Verreaux & des Murs 1860), and in the early years following European settlement (e.g. Layard & Layard 1882b) so the decline of the New Caledonian Lorikeet may have been underway for some time before Black Rats arrived. Avian malaria has been suggested as a potential cause of the species' disappearance, though it has not been documented in New Caledonia (Ekstrom *et al.* 2000). Another possibility is that the New Caledonian Lorikeet was seasonally dependent upon the sclerophyll forests along the west coast (Ekstrom *et al.* 2000), which have all but disappeared (Bouchet *et al.* 1995, Veillon *et al.* 1999). In view of its extreme scarcity, the New Caledonian Lorikeet is currently listed as 'critically endangered' by the IUCN (2011).

BIOGEOGRAPHY OF NEW CALEDONIAN PARROTS

The occurrence of five parrot taxa in New Caledonia is interesting from a biogeographical standpoint as it highlights the different origins of New Caledonia's biota. Most authors contend that the distribution of *Cyanoramphus* is the result of long-distance dispersal (Fleming 1976, Taylor 1985, Boon *et al.* 2001, Chambers *et al.* 2001). Using molecular clocks to estimate divergence dates, Boon *et al.* (2001) hypothesised that at least 20 Ma have passed since *Cyanoramphus/Eunymphicus* diverged from a common, Australian ancestor (possibly the predecessor of *Platycercus*). They estimated that *Cyanoramphus* diverged from *Eunymphicus* about 2.9 Ma ago, and proposed that *Cyanoramphus* dispersed from New Caledonia to New Zealand and surrounding islands in the last 500,000 years or so, possibly via Norfolk Island. On this basis, Chambers *et al.* (2001) considered *Cyanoramphus* to have a remarkable colonising ability. They noted, however, that this was highly unusual for parrots, an archaic group whose distribution patterns are typically associated with vicariance.

Molecular dating adds an important temporal element to biogeographic studies, but it often yields misleading results. Among the problems with molecular clocks is the assumption that evolutionary diversification proceeds at a relatively constant rate. In fact, evolution is likely to involve lengthy periods of stasis, such that there might be minimal differentiation between taxa even after millions of years of separation (Heads 2005a, b, 2009b). Molecular clocks are often calibrated based on the age of fossils or the timing of vicariant events. However, fossils only represent the minimum age of the group in question, and their value depends on how complete the fossil record is, and whether the fossils are identified correctly and dated accurately (Heads 2009b, Trewick & Gibb 2010). Likewise, correlations based on patterns of vicariance assume that the timing, and cause, of vicariance is known with certainty (Heads 2009b, Trewick & Gibb 2010). Boon *et al.* (2001) acknowledge that, in their interpretation of the evolution of *Cyanoramphus*, the estimated times of evolutionary events are best considered relative to one another than as absolute dates. Furthermore, they note that, given the potential for error in their estimates, the initial divergence of *Cyanoramphus* from an Australian ancestor could extend as far back as the Paleocene. Wright *et al.* (2008) estimated divergence times among parrot genera using a Bayesian relaxed-clock approach, with two alternative dates for the basal divergence of the New Zealand endemics *Nestor* and *Strigops* from the remaining parrots. The first date was set to 50 Ma ago, based on evidence from the fossil record of parrots, and the second date was set to 82 Ma ago, based on the separation of New Zealand and

Gondwana. The first scenario involved the colonisation of New Zealand, Madagascar, and South America by overseas dispersal from Australia, which they considered less likely. Rather, their results supported a Cretaceous origin of parrots, with vicariant diversification occurring as a result of the fragmentation of Gondwana. Under the assumption that *Nestor* and *Strigops* diverged from other parrots about 82 Ma ago, members of the Platycercini would presumably have begun diversifying in the Eocene (Wright *et al.* 2008).

As demonstrated by Wright *et al.* (2008), the branches of a phylogenetic tree can be interpreted as a sequence of dispersal to new regions, or as a sequence of differentiation in a widespread ancestor (Hedges 2009a). Based on the relationship between *Cyanoramphus* and *Platycercus*, the restricted distribution of *Cyanoramphus* in the southwest Pacific, and the exclusively Australian distribution of *Platycercus*, it could be inferred that these two groups arose from a common ancestor through vicariance (Hedges 2008). If early forms of *Cyanoramphus* were once widespread throughout Zealandia, this would account for much of its present distribution (Figure 1.4). The geologically young age of Lord Howe Island (~6.4-6.9 Ma; McDougall *et al.* 1981), Norfolk Island (~2.3-3.0 Ma; Jones & McDougall 1973), Antipodes Island (<1 Ma; Cullen 1969, Timm *et al.* 2010), and the Chatham Islands (~1.0-3.0 Ma; Campbell *et al.* 2006, 2009) suggests that they formed too recently to have provided a refuge for *Cyanoramphus* during the subsidence of Zealandia. However, the geological and volcanic history of the region is more relevant than the age of the volcanic rocks on individual islands (Hedges 2009b). All of these islands are surrounded by seamounts or plateaus that could have been emergent in the past, possibly providing habitat for parakeets and other biota until the current islands emerged. Likewise, the occurrence of *Cyanoramphus* on Macquarie Island and the Kermadec Islands might be attributed to the presence of the Macquarie Ridge and the Kermadec Ridge, which may have provided an important link to New Zealand in the past.

If the distribution of *Cyanoramphus* parakeets has been shaped by long-range dispersal, as most authors maintain, then it seems very odd that their range does not extend to Australia, Vanuatu, Fiji, Tonga, Samoa, or elsewhere in the Pacific, aside from French Polynesia. The prior existence of two species on the Society Islands is certainly the most intriguing aspect of the *Cyanoramphus* distribution. A single, overseas dispersal event seems improbable given that the islands are several thousand kilometres away from the nearest population of *Cyanoramphus* parakeets. Multiple dispersal episodes are more likely to have taken place, yet there is no trace of these parakeets on any of the islands (e.g. Tonga, Cook Islands) that might have been used as stepping stones on their way to French

Polynesia (Croizat 1958). Perhaps these are ancient lineages that arrived in the Society Islands at a time when ocean gaps were much shorter than they are today. The possibility also exists that humans have influenced their distribution through extinction and trade (Latham 1781, Olson 2006, Steadman 2006, Keogh *et al.* 2008). Molecular analyses have not been performed on either of these species, thus their relationship with other *Cyanoramphus* parakeets remains uncertain. However, Boon *et al.* (2001) suggested that they may be more closely related to *Eunymphicus* than *Cyanoramphus* based on morphological similarities.

As previously mentioned, Boon *et al.* (2001) proposed that *Eunymphicus* diverged from *Cyanoramphus* around 2.9 Ma ago. However, Heads (2008) suggested that *Eunymphicus* might have evolved much earlier, prior to the opening of the South Loyalty Basin. Given the complex geological history of the region, a number of different scenarios could potentially explain the patterns we see today. For instance, *Eunymphicus* may have evolved on the Loyalty Ridge, in geographic isolation from *Cyanoramphus*. The collision of the Loyalty Ridge with the Norfolk Ridge about 35 Ma ago (Heads 2008) might have allowed *Eunymphicus* to colonise the mainland without having to cross wide ocean gaps, and the subsequent parting of the Loyalty Basin may have led to the differentiation of *E. cornutus* from *E. uvaeensis*. Of course, the possibility exists that overseas dispersal has played a role in the evolution of *Eunymphicus*, but this is not consistent with the highly restricted distribution of this genus.

Although lorikeets also occur in New Caledonia, they clearly arrived in a different manner than the platycercines. It is generally thought that *Trichoglossus* and *Charmosyna* radiated outward from Papua New Guinea, as most of their diversity is centred on this region (Berlioz 1945, Vuilleumier & Gochfeld 1976, Forshaw 1989, Serpell 1989). The distribution of *Trichoglossus* reaches beyond that of *Charmosyna*, covering the Lesser Sunda Islands and Sulawesi to the west, and parts of Australia to the south. In contrast, the distribution of *Charmosyna* extends no farther west than the Moluccas and does not enter Australia. Both genera are distributed from the Bismarck Archipelago to Vanuatu, yet only *Charmosyna* is present in Fiji (Forshaw 2010). Serpell (1989) surmised that the main period of expansion and speciation of the lorikeets occurred no earlier than the Lower Pleistocene. Further, he argued that the expansion and radiation of *T. haematodus* probably took place during the most recent glaciation period between 60,000 and 16,000 years ago, when sea levels were lower by 100 m or more. Given that several distinct Rainbow Lorikeet subspecies are found on the Lesser Sunda Islands, yet only a single subspecies (*i.e.* *T. h.*

massena) is found on the numerous islands that span from the Bismarck Archipelago to Vanuatu, Cain (1955) reasoned that the latter region must have been colonised so recently that there has been insufficient time for extensive subspeciation to occur. Whether the expansion of *T. haematodus* occurred as recently as suggested by Serpell (1989) is debatable, however, as enough time has passed for *T. h. deplanchii* to differentiate from *T. h. massena*. This point was dismissed by Cain (1955), who considered the bluer head of *T. h. deplanchii* to be merely an 'Australian influence', as this characteristic is common to all the forms nearest Australia.

Charmosyna lorikeets appear to have reached New Caledonia along the same route as *Trichoglossus* lorikeets, although they probably arrived much earlier. Based on distribution patterns (Forshaw 2010), and morphological similarities between *C. rubrigularis* (Karkar Island, New Britain, New Ireland, and New Hanover in eastern PNG), *C. meeki* (Bougainville Island in eastern PNG; Kolombangara, Santa Isabel, Guadalcanal, and Malaita in the Solomon Islands), *C. palmarum* (Santa Cruz, Duff, and Reef Islands in the easternmost Solomon Islands; Vanuatu, except the Torres Islands), *C. diadema* (mainland New Caledonia), and *C. amabilis* (Viti Levu, Vanua Levu, Taveuni, and Ovalau in Fiji), these species probably form a monophyletic group within the genus *Charmosyna*. Each species is restricted to a cluster of islands, and their ranges do not overlap, thus it seems as though the gaps between island clusters have been effective barriers to dispersal. If each of these archipelagos was used as a stepping stone before colonising the next, then we would expect to see stepwise diversification from the Bismarck Archipelago to Fiji (Lucky & Sarnat 2010). However, as there is no clear phylogenetic pattern from west to east, this raises the possibility that the diversification of this group is due to vicariance caused by the fragmentation of the Vitiaz Arc. Such a scenario has been proposed to explain the distributions of other taxa in the region (e.g. de Boer & Duffels 1996, Duffels & Turner 2002). Unfortunately, molecular data are not available to support this assumption. However, geological reconstructions of the southwest Pacific suggest that floral and faunal dispersal along the Vitiaz Arc to Fiji was probably not difficult until the late Miocene (Duffels & Ewart 1988, Burrett *et al.* 1991, Lucky & Sarnat 2010). The biogeographical connections observed between the Vitiaz Arc and New Caledonia may reflect the history of the Loyalty Ridge, or perhaps even the d'Entrecasteaux Ridge, an extension of the Norfolk Ridge that curves to the northeast, towards Vanuatu (Heads 2008, 2010). Whatever the case may be, it appears as though *C. diadema* has had a long history in New Caledonia, which is probably measured in millions, rather than thousands of years. This

scenario implies that the expansion of the lorikeets occurred much earlier than hypothesised by Serpell (1989), although this is in accordance with recent molecular work suggesting a Gondwanan origin of parrots in the Cretaceous (de Kloet & de Kloet 2005, Wright *et al.* 2008).

THREATS TO NEW CALEDONIAN BIRDS

The main threats faced by New Caledonian birds are either directly or indirectly attributable to anthropogenic impacts, which date back to the arrival of humans in New Caledonia around 3,000 years ago (Sand 1999, Stevenson 1999, Perry & Enright 2002). The initial Lapita settlers brought about significant changes to the landscape, mainly through land clearance and repeated burning (Morat *et al.* 1986, Stevenson *et al.* 2001, Perry & Enright 2002). Since human arrival, vast areas of forest have been destroyed by fire, leading to the extension of savannah and secondary maquis (Morat *et al.* 1986, Jaffré *et al.* 1998a, 2001a, Stevenson 2004). The rate of landscape alteration accelerated in the mid 1800s with the settlement of Europeans, who cleared the lowlands for agriculture and cattle grazing, and introduced large-scale timber harvesting practices (Bouchet *et al.* 1995, Mittermeier *et al.* 1996, Stevenson *et al.* 2001). From 1865 onwards, the ultramafic areas have been subject to mineral prospecting and extraction (Jaffré 1980). Mining titles (concessions and exploitation permits) now cover nearly one-quarter (3800 km²) of the mainland, primarily on ultramafic sites (ORSTOM 1981, Bird *et al.* 1984). Open cast mining has led to the loss of large areas of natural vegetation, and the rehabilitation of mining sites has been largely unsuccessful (Mittermeier *et al.* 1996, Ekstrom *et al.* 2000, Herrera *et al.* 2007). In recent years, climate change has emerged as a new threat that could have a profound impact on New Caledonia's avian communities and ecosystems.

In addition to the loss and degradation of natural habitats, introduced species pose a serious risk to the New Caledonian avifauna. Pacific Rats (*Rattus exulans*) arrived in New Caledonia with the Lapita settlers, who transported them on their journeys throughout the Pacific, probably as a food item (Atkinson 1985, Matisoo-Smith & Robins 2004). Although Pacific Rats are known to prey upon birds (particularly eggs and chicks), the extent to which they have contributed to the decline or extinction of bird species in New Caledonia remains unclear (Atkinson 1985). In 1774, Captain Cook left a pair of dogs (*Canis familiaris*) and a pair of pigs (*Sus scrofa*) on the island (Cook 1821), which was the first of many introductions by Europeans. Both of these species pose a threat to ground-

nesting birds, like the Kagu and the New Caledonian Rail (Ekstrom *et al.* 2000, 2002). Dogs are known to kill adult Kagus, and pigs may prey upon eggs or chicks, and compete with Kagus for food (Warner 1948, Hunt 1996, Létocart 2000, Rouys & Theuerkauf 2003). Moreover, pigs alter forest structure by continually turning over the soil and uprooting seedlings (Sherley 2000). Although rats were present on Captain Cook's vessels, they are likely to have been Norway Rats (*Rattus norvegicus*), rather than Black Rats (*Rattus rattus*), and in any case, neither of these species is thought to have been introduced at that time (Atkinson 1973, 1985, Gargominy *et al.* 1996). Norway Rats, Black Rats, and House Mice (*Mus domesticus*) appear to have arrived as stowaways during European settlement in the mid 1800s (Revilliod 1913, Atkinson 1985, Gargominy *et al.* 1996). Cats (*Felis catus*) arrived around the same time, transported by mariners trying to reduce rat numbers (Gargominy *et al.* 1996). Rodents and cats are now widespread on the mainland (Rouys & Theuerkauf 2003), and probably pose a threat to the survival of many New Caledonian bird species. Aside from being predators of birds (Atkinson 1985), rats can also depress tree recruitment by eating fruit, seeds, and flowers, which affects birds indirectly by limiting forest regeneration (Campbell & Atkinson 2002).

The Little Fire Ant (*Wasmannia auropunctata*) was first reported in New Caledonia in 1972, and now occupies the lowlands of the main island, as well as various other islands in the New Caledonian archipelago, in both anthropogenic and natural habitats (Jourdan *et al.* 2001, Le Breton *et al.* 2007). The impacts of this tiny, stinging ant are only beginning to be understood, but its domination of invertebrate communities suggests that it has the potential to bring about widespread ecosystem disruption (Jourdan *et al.* 2001, Le Breton *et al.* 2003, 2007). Preliminary studies reveal a significant negative interaction between Little Fire Ants and lizards in sclerophyll forest, and anecdotal reports suggest that these ants may also impact nesting birds (Jourdan *et al.* 2001, Chartendrault & Barré 2005). Local declines of ground nesting birds (e.g. *Rallus* spp.) have been reported in areas where Little Fire Ants have become established (Jourdan *et al.* 2001), and these ants appear to reduce the survival and breeding success of Kagus (Theuerkauf & Rouys 2008).

Rusa Deer (*Cervus timorensis*) were imported from Java in 1870s for the purposes of hunting, and now occupy most of the natural habitats on the mainland, with the exception of maquis (Gargominy *et al.* 1996, de Garine-Wichatitsky *et al.* 2005). Although deer do not pose a direct threat to birds, they effectively prevent the regeneration of forests by trampling and grazing the understorey (Bouchet *et al.* 1995, Ekstrom *et al.* 2000). Hunters often light fires in savannah to increase access to the bush, and to attract deer by

encouraging the growth of fresh grass (Bouchet *et al.* 1995). The uncontrolled wildfires that routinely sweep across the lowlands during the dry season partly stem from these actions, although fires also arise through arson, land clearing for agriculture and livestock, and mining prospection (Bouchet *et al.* 1995, Jaffré *et al.* 1998b, Chartendrault & Barré 2005, 2006).

Hunting is a relatively widespread practice in New Caledonia, and although restrictions and regulations are in place to reduce its impact on native species, these are rarely enforced, and often ignored (Ekstrom *et al.* 2000). To a certain degree, the presence of deer and pigs probably reduces the hunting pressure on indigenous species (Gargominy *et al.* 1996). However, the impact that these introduced species have on the environment is severe, and the use of hunting dogs has disastrous consequences for flightless birds, like the Kagu (Warner 1948, Hunt 1996, Chartendrault & Barré 2005, 2006). Hunting of the ‘notou’ or New Caledonian Imperial Pigeon (*Ducula goliath*) is only permitted in April (Barré *et al.* 2003), and yet it continues throughout the year (Chartendrault & Barré 2005, 2006). The Cloven-feathered Dove (*Drepanoptila holosericea*) and the Metallic Pigeon (*Columba vitiensis*) are hunted regularly, although this is strictly prohibited (Delacour 1966, Chartendrault & Barré 2005, 2006). In rare circumstances, parakeets may also fall victim to the hunt, yet they are more likely to end up in the hands of collectors (Chartendrault & Barré 2005, 2006). Fortunately, the mainland parakeets occur in relatively rugged, inaccessible terrain. Thus, they have not been subjected to the same degree of trapping and trade as the Ouvéa Parakeet (Orenstein 1972, Robinet 1997, Pain *et al.* 2006, Barré *et al.* 2010).

JUSTIFICATION FOR RESEARCH

Parrots (Psittacidae) are more susceptible to extinction than most other bird groups (Bennett & Owens 1997). Of those in Australasia and Oceania, about one quarter are threatened (BirdLife International 2011). A number of parrots on islands in the Pacific are either endangered (e.g. *Cyanoramphus cookii*, *C. forbesi*, *Nestor meridionalis*, *Vini kuhlii*, *V. ultramarina*) or critically endangered (e.g. *Charmosyna amabilis*, *Cyanoramphus malherbi*, *Strigops habroptila*), and several have become extinct in recent times (e.g. *Cyanoramphus erythrotis*, *C. ulietanus*, *C. zealandicus*, *C. novaezealandiae subflavescens*, *Nestor productus*) (Boon *et al.* 2001, BirdLife International 2011). The parrots of New Caledonia are closely related to many of these species, and are likely to have similar vulnerabilities.

Parrots face a variety of threats, but habitat loss and degradation, introduced species, and capture for the pet trade stand out as being particularly detrimental to their survival (Kuehler *et al.* 1997, Wilson *et al.* 1998, Snyder *et al.* 2000, Wright *et al.* 2001, González 2003). Several biological factors also contribute to the fragility of this group, namely their long lifespans, relatively low reproductive output, and restrictive nesting requirements, as well as the poor survival rate of chicks and fledglings (Gnam & Rockwell 1991, Lindsey *et al.* 1994, Gilardi & Munn 1998, Wright *et al.* 2001, Masello & Quillfeldt 2002). Unfortunately, few parrot species have been studied sufficiently in the wild to identify the causes of their endangerment with confidence (Snyder *et al.* 2000). Parrots are generally difficult to observe in their natural habitat, and very little is known of the habits of rainforest species (Forshaw 1989). Most blend in well with the canopy, are highly mobile, and have inaccessible nesting cavities, making them difficult to spot, capture, or follow (Forshaw 1989, Gilardi & Munn 1998, Robinet & Salas 1999).

Ecological information about New Caledonia's parrots is urgently needed, yet difficult to acquire. The reasons for their observed declines are not completely understood, and while it is clear that anthropogenic impacts have played a decisive role, there is still much research to be conducted in order to prevent their situation from becoming worse. Accordingly, this study aims to contribute to the conservation of parrots in New Caledonia by providing information about their spatial ecology. Identifying relationships between threatened birds and their environment is important as it provides fundamental information about how they meet their needs for survival (Manly *et al.* 2002). Furthermore, knowledge of a species' habitat requirements can be used to recognise and manage areas for their conservation (Wintle *et al.* 2005). As GIS (Geographic Information System) technology improves, and spatial information becomes more accessible, the possibilities for analysing habitat use increase (Elith *et al.* 2006). In Chapter 2, GIS is used to examine how parrots on mainland New Caledonia select habitats at a broad spatial scale with respect to vegetation, forest cover, forest size, altitude, rainfall, and soil. By determining whether parrots prefer or avoid certain habitats, we gain a greater appreciation of where conservation effort should be focused.

To develop a comprehensive understanding of the manner in which ecological conditions influence parrots, it is useful to combine landscape-scale approaches with research at a finer scale (Wiens 1981). Thus, in Chapter 3, habitat relationships are examined in greater detail, including the selection of different vegetation types at specific sites, and how vegetation selection changes throughout the year. This is accompanied by an analysis of selection relative to forest edges, and a study of the foraging heights of each species. Understanding how certain species are influenced by habitat structure is important as it provides an indication of which species are most likely to be affected by habitat modification. As the conservation of parrots in New Caledonia is hindered by a lack of basic ecological data, the third chapter also includes a description of the activity patterns and flock sizes (including daily and monthly variations) of each species.

Obtaining reliable estimates of abundance is a pressing issue for the conservation of threatened birds. If comparisons are to be drawn between different areas or time periods, then there is a fundamental need to standardise the methods used (Dawson 1981). Surveys carried out in rainforests are particularly problematic, and yet little attention has been given to surveying birds in this environment (Lee & Marsden 2008). In Chapter 4, a standardised method of surveying parrots in New Caledonia is presented that may help to reduce some of these problems. This method is used to estimate parrot densities at several IBAs (Important Bird Areas) in order to set a baseline for future surveys, and to provide a comparative reference for densities estimated in other areas. To increase the utility of existing indices, a means of converting estimates of relative abundance into absolute densities is also presented in this chapter.

An understanding of how threatened species are distributed is useful for prioritising areas for conservation (Margules & Pressey 2000). However, as field surveys typically cover only a small part of the landscape, information about distribution patterns is often incomplete (Anderson & Martinez-Meyer 2004, Wilson *et al.* 2005). One way of overcoming this problem is to model the distribution of species based on the availability of suitable habitat (Guisan & Thuiller 2005). The primary objective of Chapter 5 is to use predictive models to infer the current and future distribution of parakeets in New Caledonia. Because population estimates play a large role in establishing the conservation status of parrots (Snyder *et al.* 2000), a secondary objective is to estimate the population size of each species by drawing upon the relationship between local abundance and modelled habitat suitability. This chapter also examines whether the existing reserve system is likely to provide adequate protection for parakeets over the long term.

Chapter 6 integrates the findings of the previous chapters into a discussion about the state of parrots in New Caledonia. Conservation measures are proposed that should help to ensure the long-term survival of New Caledonian parrots, and directions for future research are suggested.

The Appendix is comprised of a supplementary manuscript describing an audio/video surveillance system used to record and monitor nesting parakeets, and other endemic birds, in the rainforests of New Caledonia (Gula *et al.* 2010). This system has great potential, not only for studying the nesting habits of birds, but for any field situation where long-term, continuous recording is required.

**Chapters 2, 3, 4 and 5 have been removed for
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CHAPTER 6

IMPLICATIONS FOR CONSERVATION

Although parrots constitute one of the most vulnerable bird families in the world (BirdLife International 2011), comprehensive conservation strategies are lacking for many species (Snyder *et al.* 2000). Few parrots have been studied in the wild (Masello & Quillfeldt 2002), therefore little is known of the specific factors governing the survival of most species (Snyder *et al.* 2000). This thesis presents the most detailed information available to date on the abundance, distribution, and habitat of parrots on mainland New Caledonia, and provides new insights into the status of the Ouvéa Parakeet. It is hoped that this research will prove useful in the development of conservation programs for these species. This discussion deals with the implications of the findings of this study for the conservation of New Caledonian parrots, and their associated communities.

OVERVIEW AND INSIGHTS

The differences observed in the habitat preferences of New Caledonian Parakeets and Horned Parakeets are particularly interesting, from both an ecological and conservation standpoint. The two species occur sympatrically over most of their range, and yet there is no sign of interspecific competition. It appears as though their coexistence is permitted through resource partitioning, which is reflected in both their diet (J. Theuerkauf *et al.*, unpubl. data) and their habitat preferences. New Caledonian Parakeets forage mainly in the understorey and amongst early successional vegetation types, whereas Horned Parakeets typically feed in the forest canopy, or in the tops of emergent trees (e.g. *Araucaria* and *Agathis* spp.). Of the two species, the New Caledonian Parakeet appears to have a higher tolerance of, or preference for, more open habitats (e.g. maquis, slope forest, forest edges), which suggests that it may cope better with forest fragmentation. However, its tendency to forage near the ground may increase its vulnerability to ground-based predators, such as cats (*Felis catus*), especially in areas where the vegetation cover has been reduced by introduced browsers (e.g. Harrison 1970, Greene 1998, 2003). As Horned Parakeets tend to forage higher up, they might be less susceptible to these threats. Of greater concern are the effects that forest degradation may have upon Horned Parakeets as they appear to favour relatively intact forests while avoiding edges and maquis. Interestingly, the patterns of habitat segregation observed for parakeets in New Caledonia are paralleled in New Zealand, where Yellow-crowned Parakeets (*C. auriceps*) favour tall, heavily forested habitats and tend to forage in the upper strata, while Red-crowned Parakeets (*C.*

novaezelandiae) prefer forest margins and more open vegetation types, and feed at lower levels, including on the ground (Harrison 1970, Taylor 1975, Greene 1998).

The southern tip of the New Caledonian mainland provides an insight into the different habitat selection strategies employed by parakeets. New Caledonian Parakeets were regularly encountered in this region, which is comprised mostly of maquis and patchy forests on ultramafic terrain. It seems that New Caledonian Parakeets are able to cope with the fragmented nature of the forests in this area. They are not deterred by forest edges, and are often observed foraging in maquis, where they consume a variety of plants. However, they were rarely observed far from forest, and avoided areas that were sparsely forested, so their use of maquis probably depends upon the existence of nearby forests.

It is interesting that Horned Parakeets were not observed much farther south than Parc Provincial de la Rivière Bleue. In part, this appears to be due to the small size, isolation, and degraded nature of the forests in the southernmost part of the island. The deep, alluvial soils in the valley of the Rivière Bleue support tall, relatively intact forests (Jaffré & Veillon 1991), yet comparable habitats are scarce in the more open, undulating landscapes to the south. Undisturbed rainforests on ultramafic substrates are mostly located in deep river valleys and steep slopes, and probably cover less than 800 km² of the mainland (Jaffré *et al.* 2010). The patchy distribution of the Horned Parakeet in the southern third of the island appears to be at least partly attributable to the localised nature of these forests.

From surveys conducted in 1998, Ekstrom *et al.* (2000) concluded that New Caledonian Parakeets were well distributed over much of the mainland. However, of the four sites they surveyed in the Northern Province, the species was only detected at two: Mont Ignambi and Mont Colnett. No birds were recorded at Mont Panié or in the Tchamba forest to the south. Due to the small number of sites sampled by Ekstrom *et al.* (2000), the heterogeneity of the New Caledonian Parakeet distribution appears to have gone unnoticed. The present study indicates that New Caledonian Parakeets are unusually rare in the northern third of the island. In fact, they were only recorded to the west of Mont Ignambi and Mont Colnett, about 70 km to the north of any other sightings. It is not entirely clear why New Caledonian Parakeets are restricted to such a small area, though it may have something to do with the type of soils in the region. Observations of New Caledonian Parakeets were centred on a narrow band of ferrallitic soils located along the western slopes of the 'Massif du Panié' (ORSTOM 1981). It appears that forests on oligotrophic soils may act as a refuge for parakeets, particularly New Caledonian Parakeets.

However, it remains to be seen whether this is because Black Rats (*Rattus rattus*) are less abundant on soils of this nature (Rouys 2008), or whether other factors are at play.

The population estimates generated in this study suggest that approximately 5,700 New Caledonian Parakeets, and 8,700 Horned Parakeets, occur on the mainland. Given the scale of the island, and the difficulties associated with modelling habitat suitability and extrapolating densities to wider areas, these estimates are bound to suffer from various sources of uncertainty. However, there are several reasons why the size of the New Caledonian Parakeet population may genuinely be as small, or smaller, than that of the Horned Parakeet. First of all, New Caledonian Parakeets were always encountered at low densities. The maximum density recorded for this species was approximately 14 birds/km², whereas the maximum density recorded for the Horned Parakeet was approximately 32 birds/km². These densities were estimated at Parc Provincial de la Rivière Bleue, and Parc des Grandes Fougères, respectively, and are probably amongst the highest on the island. Secondly, the range of the New Caledonian Parakeet was estimated to be smaller (2,783 km²) than that of the Horned Parakeet (3,482 km²), primarily because the former species was absent from a large portion of the Northern Province. Thirdly, New Caledonian Parakeets seemed to be easier to detect than Horned Parakeets, as indicated by the relationship between encounter rates and densities for each species. Thus, unless auditory surveys have been calibrated with density estimates, they may not provide a good indication of the relative abundance of each species.

Rainbow Lorikeets were by far the most common and widespread parrot species on the mainland, therefore no attempt was made to estimate their population size, or model their distribution in this study. Rainbow Lorikeets cover large distances in flight, and their movements vary widely according to the availability of food, so it may be difficult to acquire accurate density estimates that can be extrapolated to the rest of the island. Of the New Caledonian parrots, the Rainbow Lorikeet is the species with the greatest ecological flexibility. Their ability to take advantage of both flowers and fruits (Waterhouse 1997) and their tolerance of highly modified environments appears to have allowed them to thrive in habitats that the other species typically avoid. Rainbow Lorikeets particularly favoured areas below 200 m with low rainfall and mesotrophic soils. For the most part, these are anthropogenic environments, where natural forests have been replaced by secondary vegetation, farms, orchards, villages and towns. They were also encountered in rainforests, yet forest cover was not a good indicator of their presence.

Given that parakeets have more specific habitat requirements than Rainbow Lorikeets, they are likely to be far more sensitive to environmental change. Horned Parakeets, in particular, appear to require relatively large and intact blocks of rainforest, and it is unlikely that a network of small patches would sustain viable populations of this species. Although Horned Parakeets are occasionally seen feeding in other habitats at certain times of the year, they rarely venture far from substantial rainforest patches, and seem to have little use for isolated forest remnants. Fragmentation of native rainforests probably affects this species more than any other parrot on the mainland. Its dependence upon large rainforests with tall, mature trees suggests that it might be a good indicator of forest quality. New Caledonian Parakeets also showed a strong association with forest, but compared to the Horned Parakeet, they were more inclined to use smaller patches of forest, as well as forest edges. New Caledonian Parakeets appear to be more resilient to forest degradation than Horned Parakeets, and their ability to exploit relatively open habitats in the vicinity of forest may allow them to persist in areas where the forests themselves are too small to provide a consistent supply of food. It should be noted, however, that this may have little bearing on their survival if their population is being constrained by other factors, such as predation.

Several thousand years ago, most of New Caledonia probably comprised ideal habitat for parrots. Dry sclerophyll forests occupied the plains in the west, rainforests dominated the eastern parts of the island, and maquis was restricted to small isolated patches (Jaffré *et al.* 1998a). However, much has changed since the arrival of humans, and the landscape of today no longer resembles that of the past. The dry sclerophyll forests have nearly all disappeared, and intact rainforests are mostly confined to the slopes, valleys, and summits of mountain ranges. Rainforest now covers about one-fifth of the mainland (Jaffré 1993). It harbours diverse plant and animal communities found nowhere else on earth, and provides vital habitat for most of the terrestrial birds found in New Caledonia (Ekstrom *et al.* 2000). Though it is not the only vegetation type under threat on the mainland (Jaffré *et al.* 1998a), rainforest is undoubtedly the most important for parakeets. Mining, logging, bush fires, and exotic species all threaten the integrity of rainforest, and contribute to the loss and degradation of parrot habitat by reducing the availability of nest hollows, food and shelter. If the survival prospects of parakeets are to improve, then rainforests must be protected from these threats.

Using parakeets as surrogates for biodiversity conservation may be advantageous in the short term. As charismatic birds, parakeets could help to raise support for conservation by acting as 'flagship species'. They may also serve well as 'umbrella species' because numerous organisms would benefit from the measures taken to preserve parakeet habitat (Simberloff 1998, Mace *et al.* 2006). However, if we are serious about reversing the decline of species in New Caledonia, then over time there must be a shift from single-species initiatives to approaches that maintain the integrity and diversity of natural ecosystems throughout the archipelago.

Only about 4% of the land in New Caledonia has been set aside for conservation. The diversity of plants and animals on the mainland simply cannot be protected in such a small area. Measures must be taken to integrate vulnerable ecosystems into the reserve system. The protection of intact rainforests on oligotrophic soils would be a good starting point as these areas appear to provide the most important habitat for parakeets, yet are highly susceptible to mining. Beyond this, efforts should be devoted towards conserving Important Bird Areas (IBAs), as described by Spaggiari *et al.* (2007). Terrestrial IBAs only occupy about 20% of the mainland, yet provide habitat for the majority of New Caledonian's land birds, including the most threatened species, such as the Kagu (*Rhynochetos jubatus*) (Hunt 1996) and Crow Honeyeater (*Gymnomyza aubryana*) (Ekstrom *et al.* 2002).

The existence of large and inaccessible tracts of rainforest has undoubtedly played an important role in the survival of parakeets in New Caledonia, but the fact that parakeets are scarce even in relatively pristine forests suggests that habitat loss may not be the only factor contributing to their decline. While poaching has severely impacted Ouvéa Parakeet populations (Robinet *et al.* 1995), it is unlikely to be a significant threat to parakeets on the mainland as their nests are difficult to locate, and they typically breed in relatively remote, rugged terrain. Of greater concern is the risk posed by introduced species, which are now abundant and widespread in New Caledonia (Gargominy *et al.* 1996, Rouys & Theuerkauf 2003).

The devastating effect that humans, and their commensal species, have had upon island fauna is particularly apparent in the tropical Pacific, where over 2000 bird species have likely gone extinct in prehistoric times (Steadman 1995). Since the arrival of humans in New Caledonia, at least 25% of the non-passerine birds have disappeared, and several others are known only from a scattering of reports (Balouet & Olson 1989). Along with habitat destruction and hunting, many of these species are likely to have been vulnerable to predation by the Pacific Rat (*Rattus exulans*), which arrived with the initial Lapita settlers about 3,000 years ago (Atkinson 1985). The extent of this rodent's impact on the New Caledonian avifauna remains largely unknown as the most susceptible species are likely to have disappeared long ago. Species that survived until recent times probably possessed, or developed, strategies to counter predation by Pacific Rats. It has been suggested that such behavioural adaptations may have also helped parakeets cope with predation by other rodents (Atkinson 1985, Rouys 2008). However, Norfolk Island Parakeets (*Cyanoramphus cookii*) have coexisted with Pacific Rats for about 800 years (Anderson & White 2001), and yet they remain highly vulnerable to predation by Black Rats (Taylor 1985, Forshaw 1989, Hill 2002).

Of the rodents introduced to New Caledonia, the Black Rat is the one that is most often associated with bird declines on islands around the world (Atkinson 1985). Its detrimental impact on birdlife was perhaps best demonstrated in the 1960s, when populations of eight bird species (including *Cyanoramphus novaezealandiae* and *C. auriceps*) were drastically reduced or extirpated following the arrival of Black Rats on Big South Cape Island, New Zealand (Atkinson 1985). This ecological disaster resulted in the extinction of the South Island Snipe (*Coenocorypha iredalei*) and Stead's Bush Wren (*Xenicus longipes*), and also eliminated the last known population of the Greater Short-tailed Bat (*Mystacina robusta*) (Townsend *et al.* 2006). The South Island Saddleback (*Philesturnus carunculatus carunculatus*) would have undoubtedly faced a similar fate if the few remaining individuals had not been translocated to neighbouring rodent-free islands (Hooson & Jamieson 2003).

Although the predatory abilities of rats are well documented (Atkinson 1985), their role in the decline of parakeets in New Caledonia is unclear. While Black Rats periodically visit parakeet nests, and are known to prey upon eggs and chicks, incidents of nest predation appear to be rare (Gula *et al.* 2010). Thus far, however, monitoring has only been carried out at Parc Provincial de la Rivière Bleue and Parc des Grandes Fougères.

Rouys (2008) observed that Black Rats weighed less and were relatively scarce in regions where oligotrophic soils occur, which suggests that the conditions in both of these study areas may be unfavourable for rats. It will therefore be important to monitor the nesting of parakeets living in habitats on richer soil types, especially outside of managed reserves.

The impact of rats on parakeet populations could potentially be greater than realised to date, particularly if it is compounded by other factors. Even a low incidence of rat predation might be unsustainable if parakeet populations are in decline for other reasons, such as habitat loss (Atkinson 1985). The consumption of fruits and seeds by rats might also be having an impact on the regeneration of New Caledonian forests, as has been observed in New Zealand (Campbell & Atkinson 2002). In addition, rats inadvertently affect parakeets by acting as a food source for cats (Atkinson 1985). The extinction of the Macquarie Island Parakeet (*Cyanoramphus erythrotis*) illustrates how an abundance of introduced prey can exacerbate the impacts of introduced predators on native species. For decades, parakeets coexisted with cats on Macquarie Island. However, the introduction of rabbits (*Oryctolagus cuniculus*) in 1879 led to such an increase in the number of cats, and wekas (*Gallirallus australis*), that parakeets were driven extinct by 1890 (Taylor 1979).

Compared to Horned Parakeets, New Caledonian Parakeets are likely to be more vulnerable to cats as they have a tendency to forage closer to the ground. This is supported by recent telemetry work, which indicates that fledgling New Caledonian Parakeets occasionally fall victim to cats (J.Theuerkauf *et al.*, unpubl. data). In New Zealand, the ground foraging habits of Red-crowned Parakeets (*C. novaezelandiae*) appear to have greatly increased their risk of predation, and this has possibly been a factor in their disappearance from most mainland habitats (Harrison 1970, Greene 1998, 2003). It is interesting that the closely related Yellow-crowned Parakeet (*C. auriceps*) feeds much higher above the ground (Greene 1998), and can still be found throughout the North and South Islands of New Zealand (Boon *et al.* 2001). It could be imagined that predation has also influenced the distribution of parakeets in New Caledonia. The heterogeneous nature of the New Caledonian Parakeet distribution in the Northern Province is particularly difficult to explain based solely on habitat preferences. The apparent absence of New Caledonian Parakeets near the 'Massif des Lèvres' is very unusual, as this region contains some of the most intact rainforests in the north and appears to be a stronghold for the Horned Parakeet.

Unfortunately, rats and cats are not the only introductions that raise concern. Rusa Deer (*Cervus timorensis*) and Feral Pigs (*Sus scrofa*) are now widespread in New Caledonia (Rouys & Theuerkauf 2003), and represent a potential threat to native habitats. Both of these mammals could have a detrimental effect on parakeets in the long term by altering the composition and structure of the vegetation, and influencing forest regeneration (Veillon *et al.* 1999, Ekstrom *et al.* 2002, de Garine-Wichatitsky *et al.* 2005). Honey Bees (*Apis mellifera*) were introduced in the last 60 years, and are now common throughout the main island (Kato & Kawakita 2004). Honey Bees could potentially reduce the number of available nest sites for parrots on the mainland as they are known to compete with parrots for tree hollows on Ouvéa (Barré *et al.* 2010), and elsewhere (Wiley 1985, Mawson & Long 1994, Ford *et al.* 2001). The Little Fire Ant (*Wasmannia auropunctata*) also has the potential to negatively affect nesting birds (Jourdan *et al.* 2001), and its spread may have grave consequences for New Caledonia's parrots. Since its detection in 1972 (Fabres & Brown 1978), the species has become established throughout most of the lowlands on the main island (Le Breton *et al.* 2004). Little Fire Ants occur in a variety of habitats on the mainland, including dry sclerophyll forest, rainforest (on ultramafic and acidic substrates), and maquis, and they have also been introduced to several other islands in the New Caledonian archipelago (Jourdan 1997).

Quantifying the impact of invasive species in New Caledonia is problematic because few pest-free areas remain that might serve as experimental controls (Gargominy *et al.* 1996, Rouys & Theuerkauf 2003). However, an ecological restoration program could potentially resolve any uncertainties over the extent of the problem. Restoration projects provide us with an invaluable opportunity to measure how ecosystems recover following the removal of invasive species, so it is critical that researchers are on hand to document how plant and animal species respond to their new environment. The task of measuring ecosystem-level changes can be facilitated by focusing upon organisms, such as parrots, which possess characteristics that increase their vulnerability to invasive species (Towns *et al.* 2006). In order to confirm that invasive species are reducing parakeet numbers, it would be useful to compare nesting success rates and population densities at sites with and without introduced predators, competitors, and browsers (Innes *et al.* 1999). To facilitate comparison between sites, surveys should be conducted using standardised methods, such as those presented herein. However, the control of invasive species should proceed carefully to minimise harm to native species, and to avoid upsetting an established predator-prey system (Rouys 2008). In particular, rodents and cats should be removed

simultaneously to prevent a scenario where rodents proliferate in the absence of cats, or where cats target native species as rodents decline (Towns *et al.* 1997). Ideally, browsers should be removed last so that the ensuing plant growth does not become a food source for rats (Whitaker *et al.* 2004).

RESERVE DESIGN AND MANAGEMENT

In many ways, the strategies developed to protect parrots and other wildlife in New Zealand are applicable to New Caledonia. The composition of the flora and fauna in both archipelagos is remarkably similar, and both have been subjected to a similar suite of introduced species (Towns *et al.* 1997). In addition, the parakeets of New Zealand and New Caledonia share a common ancestry (Boon *et al.* 2001), so they are likely to possess many of the same vulnerabilities. Adapting the methods used to manage and restore ecosystems in New Zealand would therefore be a very efficient approach to wildlife conservation in New Caledonia.

Although there is currently no possibility of eradicating introduced mammals from areas as large as the main islands of New Zealand or New Caledonia, eradication campaigns have been successfully implemented on many of New Zealand's offshore islands (Towns & Broome 2003). One example is that of Raoul Island, where the removal of rats (*R. norvegicus* and *R. exulans*) and cats has allowed Kermadec Red-crowned Parakeets (*Cyanoramphus novaezelandiae cyanurus*) to recolonise the island naturally, after being extirpated about 150 years ago (Ortiz-Catedral *et al.* 2009). Introduced mammals have been removed from over ninety islands around New Zealand, and the benefits of these eradications are clear (Towns & Broome 2003). However, very few of the islands in the New Caledonian archipelago have received similar treatment to date.

There is clearly a need to set aside islands for conservation, not only to preserve insular ecosystems in their own right, but also to establish supplementary populations of threatened species. However, this approach is not without its drawbacks. Translocations may fail for a variety of reasons, including the fact that habitats found on the mainland are not adequately represented on islands (Towns *et al.* 1997). Also, some islands are not easily accessed by the general public, so successful conservation efforts may go unnoticed. Unfortunately, the islands that are most likely to provide suitable habitat for parakeets in New Caledonia are large and inhabited, and eradicating invasive species from them would be a formidable task.

In New Zealand, indigenous flora and fauna are increasingly being protected *in situ* using either intensive pest control methods, or by erecting fences that exclude pests altogether (Saunders & Norton 2001). Trials are currently underway in New Caledonia to determine the feasibility of establishing an unfenced 'ecological island' at Mont Panié, which is expected to involve rigorous management of invasive species (Saunders & Wilson 2003). In spite of their high initial setup costs, fences can be a cost-effective alternative to ongoing pest control, particularly on peninsulas and in large areas where it is difficult to implement conventional pest control methods (Clapperton & Day 2001). The most ambitious mainland restoration project to date is at Mount Maungatautari in New Zealand, where over 34 km² of forest has been fenced off, and most introduced mammals have been eradicated (Speedy *et al.* 2007).

Few areas exist in New Caledonia where endemic species are not under some form of threat due to introduced mammals. The current reserve system is inadequate and provides very little tangible protection for parakeets, or for the critically endangered Crow Honeyeater (*Gymnomyza aubryana*), or the endangered Kagu (*Rhynochetos jubatus*). A relatively large, fenced 'ecological island' would be a valuable addition to the reserve system in New Caledonia. The creation of a pest and predator exclusion zone, where threatened avifauna can breed in relative safety, might mean the difference between the long-term survival and the extinction of certain species. It is troubling to think that there are no large, protected areas in New Caledonia that could potentially act as refuges in the event that remnant populations are discovered of critically endangered species like the New Caledonian Lorikeet (*Charmosyna diadema*), New Caledonian Rail (*Gallirallus lafresnayanus*), or New Caledonian Owlet-nightjar (*Aegotheles savesi*).

As fencing is expensive, there will be limitations on what can be achieved with this approach to conservation, particularly with respect to the area that can be protected. However, even small restoration projects have merit because they give us an idea of what is possible while providing a safe haven for numerous species that are on the decline, and they can act as a baseline for measuring the impact of invasive species. At certain sites, fencing could be used sparingly to safeguard the breeding grounds of threatened birds, or to protect rare organisms with restricted ranges. Fenced areas could also form the core of large reserves, acting as reservoirs of biodiversity for the surrounding areas. This approach could potentially be implemented in Parc Provincial de la Rivière Bleue by positioning fences along existing roads and trails. Many prospecting tracks already exist in New

Caledonia, and those that form a loop around high-quality rainforest could be used as a baseline for fence construction.

Landscape connectivity is a fundamental component of reserve design (Ferrier 2002). It is not enough to protect individual areas, conservation planners must also ensure that reserves provide species with dispersal opportunities. Parakeets, in particular, will require an extensive network of forested reserves to meet their needs throughout the year, and to maintain viable populations. Corridors help to maintain and restore natural connections in the landscape (Beier & Noss 1998), and should be included in the design of new reserves. For many species in New Caledonia, suitable habitat is scarce in the most accessible regions, particularly at lower altitudes. Unless measures are taken to restore habitat and prevent fires in these areas, there is a risk that more and more species will become confined to isolated mountain tops and steep valleys. As pointed out by Hunt (1996), this is already a concern for Kagus at Pic Ningua, Dent de St. Vincent, Mont Cidoa, and Koum. Corridors would be particularly useful in the far south, to facilitate the movement of New Caledonian Parakeets between forest patches. As temperatures increase with climate change, species' distributions are expected to shift upwards, and towards the poles (Wilson *et al.* 2005). Thus, it is critical that the reserve network spans entire elevation gradients and provides safe routes for species to disperse from areas that are currently isolated (Politi & Rivera 2005). Expanding the reserve network will not only increase the dispersal opportunities for species that are vulnerable to climate change, it could also help to mitigate climate change by preventing rainforest loss (Gullison *et al.* 2007).

If New Caledonia is to move towards a future that is both economically and environmentally sustainable, the short-term economic gains resulting from environmentally destructive practices must be carefully weighed against the long-term advantages of keeping ecosystems intact. The importance of natural ecosystems lies not only in the goods they supply (e.g. minerals, timber, food, and medicinal plants), but also in the services they provide (e.g. air and water purification, climate regulation, nutrient cycling, erosion reduction, flood mitigation, carbon sequestration, biodiversity protection, etc.). These services have immense economic value (Costanza *et al.* 1987, Mittermeier *et al.* 2003), yet they are often taken for granted because they come at no cost. To continue to benefit from these services, the ecosystems providing them must be maintained. What policy makers in New Caledonia have failed to recognise is that sustainable resource use and sound environmental management can be compatible with economic growth.

New Caledonia has many natural and cultural attractions, including a large lagoon, numerous beaches, tribal villages, abundant rivers, tropical rainforests, and exceptional flora and fauna. With appropriate planning, development, and marketing, the region could become a model ecotourism destination. New Caledonia's birds, and particularly parrots, have the potential to attract tourists from around the globe, yet their future depends upon the availability of suitable habitat. Ecotourism could contribute to the protection of the natural environment while providing an economic alternative for local communities. In this context, reserves should be viewed not as barriers to development, but as valuable assets that are integral to the success of ecotourism programs.

One initiative that could potentially help to balance conservation and development in New Caledonia is UNESCO's 'Man and the Biosphere' program, which promotes environmental sustainability through a global network of biosphere reserves. Biosphere reserves are sites that aim to conserve natural and cultural diversity, while fostering environmentally sustainable social and economic development, and facilitating environmental education, research, and monitoring (UNESCO 1996). Each biosphere reserve is typically divided into three zones: core areas, where ecosystems are carefully protected and only activities that have minimal impact on the environment are allowed (e.g. monitoring, research, and education); buffer zones, where ecologically sound activities are generally permitted (e.g. ecotourism, recreation, and applied research); and transition areas, where various organisations, community groups, and stakeholders combine efforts to sustainably manage the natural resources in the region (UNESCO 1996). In New Caledonia, biosphere reserves could potentially be set up with high-quality or primary rainforest as core areas, surrounded by a buffer of medium-quality or secondary rainforest, and eventually transitioning into lower-quality forests, savannah, or maquis. By establishing reserves in this manner, the most vulnerable ecosystems would receive the greatest level of protection, and sustainably managed activities, such as agroforestry and hunting, could continue in the peripheral areas without causing undue disruptions to fragile environments. This approach to reserve creation may be particularly appropriate for the 'Rivières Néoua, Koua, & Kouaoua' IBA, as it appears to be one of the most important sites for parakeets, yet conservation strategies will need to incorporate the needs of the Néoua tribe, which holds the customary rights to much of the forest in this region (Ekstrom *et al.* 2000). Biosphere reserves could also be established at the 'Massif du Panié' and 'Massif des Lèvres', in consultation with local tribes. These two areas contain the largest contiguous

tracts of rainforest remaining in the Northern Province, and are critical sites for parakeet conservation in the north.

New Caledonia's tropical rainforests might also qualify for UNESCO World Heritage listing on the basis that they provide important habitat for threatened species of outstanding scientific and conservation value (UNESCO 2008). A World Heritage listing would raise awareness of the international significance of New Caledonia's biodiversity, and instil a sense of responsibility among local inhabitants and provincial governments to protect the natural environment. Local communities would likely experience a number of benefits from inscribing a site on the World Heritage List, including a rise in tourism, increased employment opportunities, and access to funds that help to protect and manage such sites.

CONSERVATION PRIORITIES

Based on the results of this study, the following measures are recommended to preserve habitat for parakeets in New Caledonia:

- (1) Protect relatively intact forests at moderate altitudes (200-800 m) on oligotrophic soils as these areas provide important habitat for both species. Priority should be given to the protection of forests on ultramafic massifs as these are most vulnerable to mining activity. In particular, 'Réserve Spéciale de Faune et de Flore de Nodela' should be enlarged to include the remaining forests on the 'Massif du Mé Maoya'.
- (2) Extend the boundaries of 'Parc des Grandes Fougères' so that it incorporates the remainder of the 'Table Unio' IBA. As this is a critical site for parakeets, some vigilance may be required to ensure that conservation efforts are not undermined by the nearby hunting reserves.
- (3) Establish a reserve based on the 'Rivières Néoua, Koua, & Kouaoua' IBA. This region harbours substantial populations of New Caledonian Parakeets and Horned Parakeets, yet special measures may be required to achieve conservation goals without impinging on the needs of the local community.

- (4) Create reserves that encompass the 'Massif du Mé Kanin, Sphinx & Arago' IBA, as well as the IBAs adjoining Mont Canala and Mont Nakada. These areas all provide important habitat for both parakeet species.
- (5) Expand the 'Réserve Spéciale Botanique du Mont Panié' to include the rest of the 'Massif du Panié', and upgrade its conservation status to a 'Réserve Spéciale de Faune et de Flore', or similar. This reserve would then comprise the largest contiguous block of forest in the Northern Province. Although New Caledonian Parakeets and Horned Parakeets occupy the 'Massif du Panié', none were recorded in the current reserve. The population of New Caledonian Parakeets on the 'Massif du Panié' appears to be isolated, and deserves appropriate protection.
- (6) Establish a reserve at the 'Massif des Lèvres'. This region is remote, isolated, and contains the second largest area of forest in the Northern Province. The 'Massif des Lèvres' is also a stronghold for Horned Parakeets.

Unfortunately, New Caledonia's ecological problems will not be solved merely by setting aside land for conservation. Most conservation areas will require some form of management, or at least a monitoring program aimed at identifying issues as they arise (Kepler & Scott 1985). Ideally, the outcome of management procedures should be measurable so that the effectiveness of different approaches can be gauged (Innes *et al.* 1999). At most reserves, there will be a need to control introduced plants and animals, minimise the risk of fire, and enforce restrictions on hunting, harvesting, and poaching. To have the best chance of success, members of the local community should be actively involved in the entire management process (Saunders & Wilson 2003). Ultimately, the survival of parrots depends upon our ability to preserve and manage suitable habitat. The challenge is to incorporate what we know about their habitat preferences into conservation initiatives that will have a long-term impact.

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